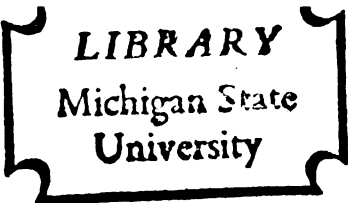RESPONSES IN YIELD AND YIELD
COMPONENTS FROM RECURRENT SELECTION
PRACTICED IN A BEAN HYBRID
POPULATION AT THREE LOCATIONS IN
NORTH AND SOUTH AMERICA

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
Rodrigo A. Duarte
1966

This is to certify that the

thesis entitled

RESPONSES IN YIELD AND YIELD COMPONENTS FROM RECURRENT
SELECTION PRACTICED IN A BEAN HYBRID POPULATION
AT THREE LOCATIONS IN NORTH AND SOUTH AMERICA

presented by

Rodrigo A. Duarte

has been accepted towards fulfillment
of the requirements for

___Ph.D.___ degree in_Crop Science

W. W. Adams
Major professor

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O-169

ABSTRACT

RESPONSES IN YIELD AND YIELD COMPONENTS FROM RECURRENT
SELECTION PRACTICED IN A BEAN HYBRID POPULATION
AT THREE LOCATIONS IN NORTH AND SOUTH AMERICA

By Rodrigo A. Duarte

The population studied originated from an intra-specific

cross of Phaseolus vulgaris variety Algarrobo by variety

Michelite. Algarrobo is a kidney bean variety native to Colombia,

South America and Michelite is a navy bean variety from Michigan.

These two varieties possess contrasting characteristics not only

in leaf area components namely, number of leaflets per plant (N)

and size of the leaflets (S), but also in yield (W) components,

namely number of pods per plant (X), number of seeds per pod

(Y), and seed weight (Z).

Recurrent selections methods were applied to this popula-

tion with the aim of producing sets of lines with high levels

(A) of each component, intermediate (M) levels, and low (B)

levels. Results from two cycles of selection are reported in

this thesis.

The experiments were conducted at three locations, two of

them Palmira and Medellin in Colombia, S.A., and the third one

East Lansing in Michigan, U.S.A. These locations differ in cli-

matic conditions such as temperature, rainfall, etc.

Selection in Colombia was practiced independently for N, S,

X, Y, and Z. In Michigan, selections were made for each of X, Y,

Z and also W. Identical selection criteria were used at all

locations.

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The results show clearly that great progress due to selection was made for each one of the components of the complex traits under study. The rate of progress for each particular component at either the high or low level of expression was not the same at each location. Genotypic ―environmental interactions at the three different locations are inferred. There was a tendency toward preferential recovery of the Algarrobo type in the selected families in Colombia, and of the Michelite type in Michigan.

Comparing the average values of yield in grams per plant when selections were made independently for X, Y, Z and W at high and low levels, it was observed that all values at each level were practically the same. Progress for yield itself was not really made. Progress of individual components was obtained but the progress in one component was at the expense of another or other components, giving through the multiplicative interaction comparable seed yields. Although yield is modified by environmental forces, it shows homeostatic stability to offset the force of component selection in any direction, high or low.

The unselected components present a similar pattern of variation at all locations during the two cycles of selection.

They exhibited negative relationships with the selected ones,
the magnitude of the association depending upon the response to
selection. Due to the fact that in the second cycle more pro-
gress was made in the selected components, the negative associations
with the unselected ones were more pronounced; however, if one of
the unselected characters shifted too far in a direction opposite
to the selected one the third component shifted in the same direction
as the selected, stabilizing in this manner the final product: yield.
This pattern of relational symmetry and reversion toward the modal
class for the non-selected components was typical of all locations.

The idea of negative associations among components was
supported by the correlation coefficients obtained; however, the
sign of these correlations changed from one cycle of selection to
the next, suggesting that the effect of selection and/or environ-
ment can change the degree of relationship among components.
These findings are in good agreement with results obtained
by other authors , and strongly suggest that these correlations
are not truly genetic. It also furnishes evidence indicating that
mainly independent genetic systems are controlling each one of the
yield components in beans.

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Two hypotheses are presented to explain the negative associations, both based on the idea that the yield components share a common pool of resources for their development. Both hypotheses assign an important role to the manner of distribution of resources to the developing components. In one hypothesis the distribution of resources would depend on the interaction between the genotype of each component and resource-producing genes. These interactions, which take the form of de-repression or "turning on" processes, occur prior to floral development.

Fundamental to the second hypothesis is the fact that yield components follow a sequential pattern of development, each having its own genetic system. If a proportionately greater share of the resources were used in producing high X, a proportionately lesser amount would be available to produce high Y values or possibly Z values which follow X in the time sequence of development. Selecting for a component such as Z its high expression would depend on plentiful resources which implies genotypes of low levels of expression for Y and Z.

Path coefficient analyses were made in order to obtain information of the direct and indirect effects of N and S upon the yield components X, Y, and Z, and the effect of the latter components upon yield (W). The high value of the positive correlation between N and X is made up mostly of direct effects indicating the great

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influence that N has in determining X. The main direct effect of S is upon Z; X exerts the greatest influence upon seed yield; followed by Y, then by Z. The magnitude of the direct effects of each one of the components was enhanced by recurrent selection. The fact that N has a large direct effect upon the determination of X, and S upon Z gives support to the hypothesis of the "turning on" of genes before floral development.

RESPONSES IN YIELD AND YIELD COMPONENTS FROM RECURRENT

SELECTION PRACTICED IN A BEAN HYBRID POPULATION

AT THREE LOCATIONS IN NORTH AND SOUTH AMERICA

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INTRODUCTION

Progress has been made in crop yield improvement without clear-cut genetic information on the inheritance of grain yielding ability. It has been expected that as new genetic information was obtained, it would lead to greatly increased efficiency in selection programs, that in turn would lead toward greatly-increased upper yield levels.

During recent years plant breeders have devoted more attention to the study of the individual components of complex traits such as yield with the purpose of gaining a greater understanding of the genetic mechanisms that control these traits.

To date it has been clearly demonstrated that certain complex traits often may be viewed as artifacts made up by the multiplicative interactions of their components. Moreover the heritability of the complex characters has been shown frequently to be low, and the heritability of the components to be, in general, higher.

Seed yield in beans is a complex trait made up by number of pods per plant (X), number of seeds per pod (Y) and average seed weight (Z). So is total leaf area which is comprised of number of leaflets per plant (N) and average leaflet size (S).

With the purpose of producing by means of selection sets of lines with the individual components represented at different levels of expression, high, intermediate, and low, recurrent selection methods were used. It is well known that recurrent

selection is a powerful tool to increase the frequency of desirable genes and gene combinations in a plant population, although it has not been used extensively in self-fertilizing species.

Environmental conditions interacting with the genetic make up of the components of complex traits, can produce different phenotypic effects. In view of such interations and in order to see if results of selection at one location bore any similarity to results obtained at another location, this study was conducted at two places in Colombia, South America and in East Lansing, Michigan. Moreover, one of the parents of the hybrid population under study originated in Michigan and the other is of Colombian origin.

The purpose of this thesis was to obtain a fuller knowledge with respect to the response to selection, in quite different environments, of each one of the components of the complex traits; of equal importance was the desire to obtain a better understanding of the relationships between the selected and non-selected components, relationships of great concern for they fix the final product - yield.

Of greater importance to the plant breeder is to get more knowledge about the direct and indirect contributions of each one of the components in determining the complex trait. To contribute to this knowledge, path coefficients analyses were made to determine the direct and indirect influence, of X, Y and Z upon W, and also the effects that N and S could have upon the yield components.

REVIEW OF LITERATURE

Yield in oats has been interpreted by Grafius (4) as the volume of a rectangular parallelepiped, whose edges are the yield components: the number of panicles per unit area X, the average number of kernels per panicle Y, and the average kernel weight Z. It was pointed out that the edge most subject to change would be the longest and that changes in the components or edges would tend to counterbalance.

Working with cotton, Hutchinson (6) partitioned yield into bolls per plant, seed cotton per boll, seeds per boll, and lint per seed. Environmental variations seemed to affect some characters more greatly than others, and selection was found to be more effective for certain components. This work was the first to show clearly in a selection experiment the compensatory variation that develops among components; that is, the intensification of one character that can only be obtained at the expense of the others because of "physiological incompatibilities".

Whitehouse et al (12) reported upon yield components of wheat using as the components: weight per grain, grains per spikelet, spikelets per ear, and ears per plant. Correlation analysis between components were made, and it was found they were completely independent of each other. Yield predictions by means of diallel crosses, in which the best varieties for yield components were chosen, was also mentioned.

Camacho et al (2) studied genotypic and phenotypic correlations of components of yield in kidney beans. The authors found that all correlations between yield components were negative but that yield was positively correlated with its components. From the genotypic correlations they concluded that an increase in pod number caused a decrease in number of beans per pod, and that an increase in the latter component was reflected in a reduction of bean size.

Response to selection for yield in cotton was analyzed by Manning (7) using the yield components designated by Hutchinson. He found considerable genetic variability in the material after seven generations of self-fertilization. Of particular interest was the improvement of the modal-class bulk (intended as a stable population from which to measure selection gains) which suggests that natural selection favors the breeder whenever the number of seeds produced is intimately related to yield.

According to Olsson (9), no correlation would be demonstrated between the seed yield of an individual plant and the yield of a progeny plot in Brassica and Sinapis. In regard to number of seeds per pod and seed size however an evident correlation between mother and progeny was found, suggesting adaptive modifications of pod number between parental plants and their progeny in plots. The author also reported the tendency toward a decrease in seed weight when number of seeds per pod were increased and that selection for low number of seeds resulted in a decrease in fertility.

In a two-year study of corn yield and its components-ear number, number of kernel rows, kernels per row and kernel weight-Hoen and Andrew (5) found significant positive correlations between yield and its components. Ear number showed no correlation with kernels per row or kernel weight. No correlation between kernel rows with kernels per row or kernel weight was observed; however, a significant negative correlation was detected between kernels per row and kernel weight during one year out of two.

Archibong (1) studied the influence of spacing and inter-strain competition in navy beans. He found that the stress of competition caused significant changes in the pattern of relation-ships among the yield components of the several genotypes.

MATERIALS AND METHODS

Intra-specific crosses of Phaseolus vulgaris variety Algarrobo by variety Michelite were produced. These two varieties possess contrasting characteristics, which can be summarized as follows:

Characteristics	Algarrobo
Origin	Colombia, S.A.
Type of seed	Mottled kidney bean
Type of growth	Determinate (bush)
Number of leaflets per plant (N)	Few
Size of the leaflets (S)	Large
Number of pods per plant (X)	Few
Number of seeds per pod (Y)	Few
Seed weight (Z)	Heavy

Characteristics	Michelite
Origin	Michigan,U.S.A.
Type of seed	Navy bean
Type of growth	Indeterminate (vine)
Number of leaflets per plant (N)	Many
Size of the leaflets (S)	Small
Number of pods per plant (X)	Many
Number of seeds per pod (Y)	Many
Seed weight (Z)	Light

Crosses were made under greenhouse conditions in 1959-60 and F_1 and F_2 progenies were grown in that environment in order to produce F_2 and F_3 generations for planting in the field. Seed coming from the F_3 generation was divided in three parts to be planted on land of the Agricultural Experiment Stations at Palmira and Medellin (Colombia, S.A.) and at the Michigan Agricultural Experiment Station in East Lansing, respectively. Palmira is located at 1,000 mts. over sea level, with an average temperature of 25°C. and rainfall of 1,000 m.m. per year; Medellin with an

average temperature of $21^{o}C$. and rainfall of 1,300 m.m. is situated
at 1,500 mts. over sea level.

One hundred and twenty one F_4 families were planted in February
1962 at Palmira and Medellin and during the summer of the same year
at East Lansing. Each family was planted in an individual row,
with 3 replications, using 20 plants per replication with a 6-inch
spacing between plants within rows.

Selections in Colombia were practiced for components of Total
Leaf Area (T), namely, number of leaves per plant (N) and size of
the leaves (S), and for yield (W) components, namely, number of pods
per plant (X), number of seeds per pod (Y), and average seed
weight (Z). In East Lansing, selection was practiced independently
for each of X, Y, Z and W.

Selections were made at three levels of expression for each of
the characters under study. The levels were: high (A), inter-
mediate (M), and low (B).

Four families were selected for each character, at each level,
giving a total of 60 families in Palmira, 60 in Medellin and 48 in
East Lansing. For the high (A) and low (B) selections the extremes
were taken, i.e., the 4 highest and the 4 lowest in the population
for any component. The intermediate or modal-class selections
were restricted to families within one (1) standard deviation centered
on the mean.

Leaf area (S) measurements and leaf counts (N) were made two
weeks after the onset of flowering, taking two plants at random per
family per replication. At maturity number of pods per plant (X),

and number of seeds per pod (Y), were recorded in a 3-foot section of the row. In order to obtain the average weight of a seed (Z), a sample of 100 seeds was taken.

With the aim to produce by recurrent selection methods sets of lines with high levels of each component, with intermediate levels of each component, and with low levels of each component, crosses were made among components at each level. That is, considering yield components, plants in families with high number of pods per plant (XA) were crossed with plants in families having high number of seeds per pod (YA) and with plants in families having high seed weight (ZA), doing the same thing with YA and ZA. To illustrate this point, calling XA-1, XA-2, XA-3, XA-4 the four selected families for high number of pods, and YA-1... YA-4, ZA-1... ZA-4 the four selected families for high number of seeds per pod and high seed weight, respectively, the following kinds of crosses were performed.

```
        YA-1                        YA-1
XA-1 YA-2              XA-3  YA-2
        YA-3                        YA-3
        YA-4                        YA-4


        YA-1                        YA-1
XA-2 YA-2              XA-4  YA-2
        YA-3                        YA-3
        YA-4                        YA-4


        ZA-1                        ZA-1
XA-1 ZA-2              XA-3  ZA-2
        ZA-3                        ZA-3
        ZA-4                        ZA-4


        ZA-1                        ZA-1
XA-2 ZA-2              XA-4  ZA-2
        ZA-3                        ZA-3
        ZA-4                        ZA-4


        ZA-1                        ZA-1
YA-1 ZA-2              YA-3  ZA-2
        ZA-3                        ZA-3
        ZA-4                        ZA-4


        ZA-1                        ZA-1
YA-2 ZA-2              YA-4  ZA-2
        ZA-3                        ZA-3
        ZA-4                        ZA-4
```

In the same manner, crosses for intermediate expressions of yield components, namely, XM, YM, ZM, and for low expressions XB, YB, ZB, were made.

In addition, in Palmira and Medellin, crosses were performed between families with high number of leaves per plant, NA-1...NA-4, and families with large size of leaves SA-1..SA-4, and similarly for families with intermediate and low levels of expression, namely: NM-1...NM-4, SM-1...SM-4 and NB-1 ... NB-4, SB-1 ... SB-4. Seeds resulting from the one hundred and ninety two possible combinations of crosses made were planted in the

field in the two locations in Colombia. An average of seven F_1 plants were grown per each combination, coming from 2 or 3 artificially pollinated pods.

In East Lansing, selections on the basis of yield (W) itself were made, besides the selections for yield components X, Y, and Z. Crosses of yield-component selections were performed following the same program described above. Families selected for W were intercrossed among themselves, but not with X, Y and Z.

One hundred and sixty two possible combinations were obtained and from 3 to 4 F_1 plants were grown in the greenhouse, per each combination.

The F_2 generation produced in preparation for the second cycle of selection was grown under field conditions. In Palmira and Medellin 192 F_2 plots were planted with an average of 30 plants per plot.

On visual criteria, but not with actual measurements, 4 plants per each of the F_2 plots, were chosen in order to give rise to the F_3 generation. In some cases it was not possible to get 4 plants so 1, 2 or 3 were selected. These selections were based on 3 levels of expression (A - M - B) and the characters under consideration (N, S, X, Y, Z and W). The first third of the F_2 population was made up of families with high level of expression (A), the second third of families with intermediate levels (M) and the third part of families with low levels (B).

Seven hundred and sixty eight F_3 families were grown in Medellin; 532 in Palmira and 410 in East Lansing. Planting methods, selection procedures and selection pressures were the same as in the first cycle of selection, already discussed.

Since in Colombia there are two growing seasons per year in contrast to Michigan that has only one, the schedule of crossing and selection events in the two places was arranged somewhat differently. The final selections of the 2nd cycle were made during the fall of 1964 in Colombia, and during the summer of 1965 in East Lansing.

For the purpose of this thesis two cycles of recurrent selection are considered. However, this study will continue until the 3rd or 4th cycle. At the end of this time all resulting lines from all cycles will be grown at all locations for one year to see what has been accomplished by the different levels of selection.

EXPERIMENTAL RESULTS AND DISCUSSION

I. Response to Selection

A. Number of Leaflets for Plant (N)

Tables 1.1 and 1.2 contain t-test comparisons of gains between
the first and second cycle of recurrent selection, for high (NA)
and low (NB) number of leaflets per plant respectively, at Palmira
and Medellin. For these tables and for the following ones, the
mean values of the selected families are expressed on a percentage
basis with the mean of the modal class selections being taken as
100 percent in each one of the cycles. In this way, changes in
means due to variation in environmental conditions prevailing
during each cycle of selection are minimized.

Figure 1 shows graphically the response to selection from
the first to the second cycle of recurrent selection for high (NA)
and low (NB) levels of expression of number of leaflets per plant,
at Palmira and Medellin as compared to the modal class on the
percentage basis.

Highly significant differences between cycles for NA were
observed at Palmira as well as at Medellin. Ninety nine and thirty
three relative units of progress were obtained at Medellin and
Palmira respectively (Figure 1). For the purpose of this thesis
the difference between the average percentage in the first and
the second cycle is called relative units of progress.

Selections for a lower number of leaflets per plant show highly
significant differences at Palmira. Progress toward a lower number

of leaflets was made at Medellin, but the difference was not significant by the t-test. In these two locations twenty two and twelve relative units of progress toward the lower level were obtained.

Table 1.1 - t-tests, and mean values of families selected for high number of leaflets per plant (NA), in two cycles of recurrent selection at Palmira and Medellin. Data are expressed as percentage of the modal class.

| Locations | Values of 4 selected families | | t-values |
	1st cycle	2nd cycle	
Palmira	143.05	182.37	
	144.94	181.51	
	159.06	180.65	
	144.00	177.20	
Average	147.76	180.43	8.27**
Medellin	151.94	230.53	
	151.04	230.53	
	150.90	256.99	
	132.09	264.55	
Average	146.49	245.65	9.84**

**P < .01

Table 1.2- t-tests, and mean values of families selected for low
number of leaflets per plant (NB), in two cycles of
recurrent selection at Palmira and Medellin. Data
are expressed as percentage of the modal class.

| Locations | Values of 4 selected families | | |
	1st cycle	2nd cycle	t-values
Palmira	67.76	39.57	
	68.71	44.73	
	64.94	41.29	
	64.94	52.47	
Average	66.59	44.52	7.08**
Medellin	53.40	54.80	
	59.27	48.19	
	59.73	39.68	
	61.68	41.57	
Average	58.52	46.06	1.45

**P < .01

B. Leaflet Size (S)

Mean values of the selected families and t-tests, for the two
cycles of recurrent selection, at Palmira and Medellin for large
(SA) and small leaflet size (SB) are shown in Tables 2.1 and 2.2,
respectively. Rate of progress between cycles at Palmira and Medellin
is presented in Figure 2.

From table 2.2 it appears that no significant differences were
obtained between the two cycles for selections of small leaflet sixe
(SB) in either one of the two locations. However, 14 relative
units of progress for SB at the end of the 2nd cycle were obtained
in Palmira; on the contrary in Medellin, even though 14 units of
change were observed, this change was opposite to the direction of
selection. These results are presented graphically in Figure 2.
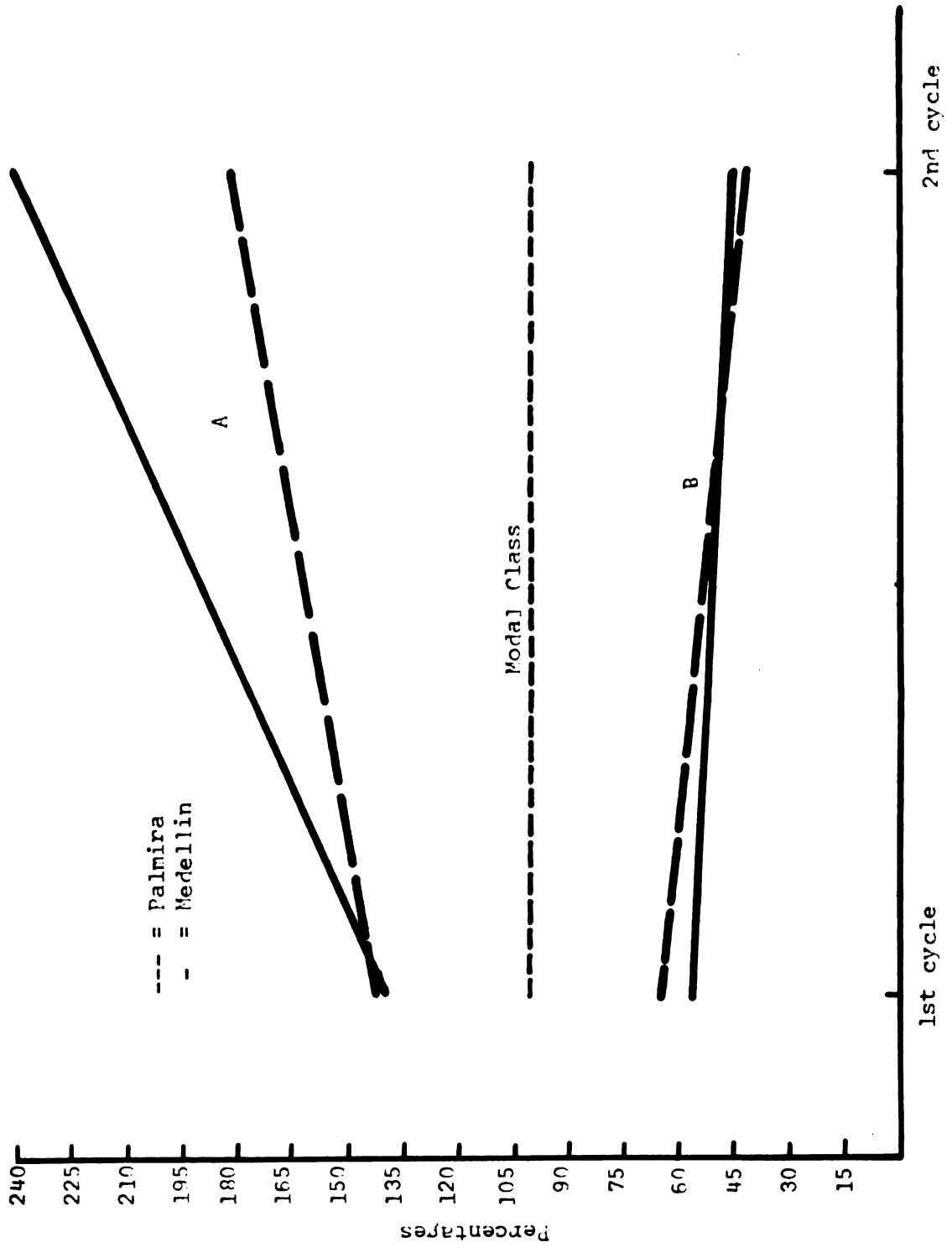
Figure 1. Response to two cycles of recurrent selection for high (A) and low (B) level of expression of number of leaflets per plant (Y), at Palmira and Medellin. Data are expressed as percentage of the modal class.

Table 2.1   t-tests and mean values of families slected for high
            size of leaflets per plant (SA), in two cycles of
            recurrent selection at Palmira and Medellin. Data
            are expressed as percentage of the modal class.

| Locations | Values of 4 selected families | | |
	1st cycle	2nd cycle	t-values
Palmira	153.35	252.13	
	150.39	250.35	
	146.11	218.39	
	138.92	229.04	
Average	147.19	237.48	10.23**
Medellin	187.50	211.43	
	183.25	234.51	
	169.02	240.70	
	156.48	222.86	
Average	174.06	227.38	5.56**

**P < .01

Table 2.2   t-tests and mean values of families selected for low
            size of leaflets per plant (SB) in two cycles of
            recurrent selection at Palmira and Medellin. Data
            are expressed as percentage of the modal class.

| Locations | Values of 4 selected families | | |
	1st cycle	2nd cycle	t-values
Palmira	59.66	39.77	
	59.31	48.65	
	67.98	60.72	
	69.63	49.71	
Average	64.14	49.71	2.84
Medellin	41.64	60.70	
	58.14	73.80	
	59.90	79.05	
	65.34	67.62	
Average	56.25	70.29	2.17
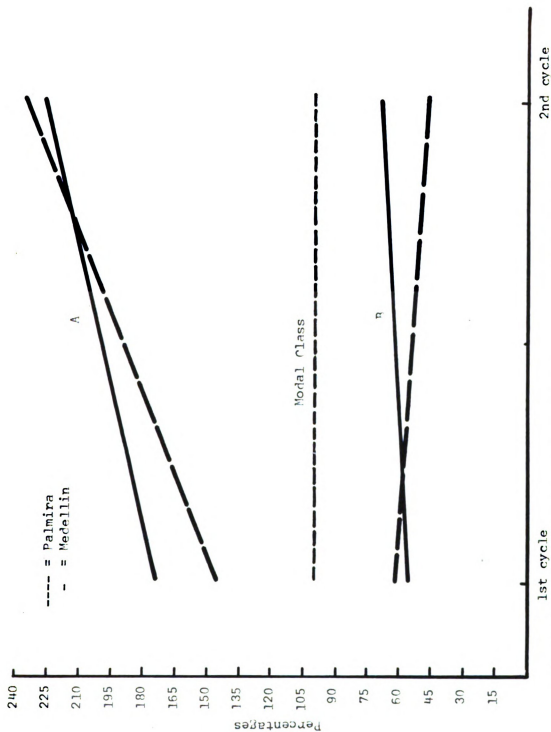
Figure 2. Response to two cycles of recurrent selection for high (A) and low (B) level of expression of size of leaflets (S), at Palmira and Medellin. Data are expressed as percentage of the modal class.

C. Number of Pods Per Plant (X)

Tables 3.1 and 3.2 contain mean values of selected families
in the two cycles of recurrent selection for high (XA) and low
(XB) number of pods per plant at three locations: Palmira, Medellin
and East Lansing. Progress in selection between the two cycles
is shown graphically in Figure 3, at three different locations,
and two levels of expression, XA and XB.

A highly significant difference between cycles for XA was
obtained at East Lansing, a significant difference at the 5 per-
cent level, and no significant difference were obtained at
Palmira and Medellin, respectively, as may be seen in Table 3.1.

In selecting for high number of pods per plant (XA) the
greatest gain was obtained at East Lansing with 70 relative units
of progress between the first and the second cycle; sixty and 30
relative units were obtained at Palmira and Medellin, respectively.

Selections for XB proved to be significantly lower at the end
of the 2nd cycle as compared with the 1st cycle, at the 1 percent
level of significance in Medellin and East Lansing, and at the 5
percent level of significance at Palmira, as shown in Table 3.2.

Figure 3 shows graphically the progress made in selecting for
XB from the 1st to the 2nd cycle. Forty-four relative units of gain
were obtained at Medellin, 17 in Palmira and 14 in East Lansing.

Table 3.1 t-tests and mean values of families selected for
high number of pods per plant (XA), in two cycles of
recurrent selection at Palmira, Medellin and East
Lansing. Data are expressed as percentage of the
modal class.

| Location | Values of 4 selected families | | t-values |
	1st cycle	2nd cycle	
Palmira	154.82	260.14	
	142.19	213.84	
	148.83	182.82	
	155.48	182.82	
Average	150.33	209.91	3.22*
Medellin	172.12	166.67	
	143.03	236.08	
	143.03	142.83	
	138.18	171.42	
Average	149.09	179.25	1.41
East Lansing	143.10	220.50	
	143.60	211.50	
	144.00	213.90	
	144.50	209.00	
Average	143.80	213.70	28.09**

* $P < .05$
** $P < .01$

Table 3.2 t-tests and mean values of families selected for low
number of pods per plant (XB), in two cycles of
recurrent selection at Palmira, Medellin and East
Lansing. Data are expressed as percentage of the
modal class.

| Locations | Values of 4 selected families | | t-values - |
	1st cycle	2nd cycle	
Palmira	58.47	42.72	
	65.78	35.80	
	59.80	40.57	
	48.50	44.15	
Average	58.14	40.81	4.20*
Medellin	56.97	8.33	
	59.39	25.00	
	61.82	14.16	
	64.24	16.67	
Average	60.60	16.04	11.74**
East Lansing	51.10	36.80	
	44.50	31.10	
	50.20	35.20	
	53.70	38.50	
Average	49.90	35.40	5.79**

* P <.05
** P <.01
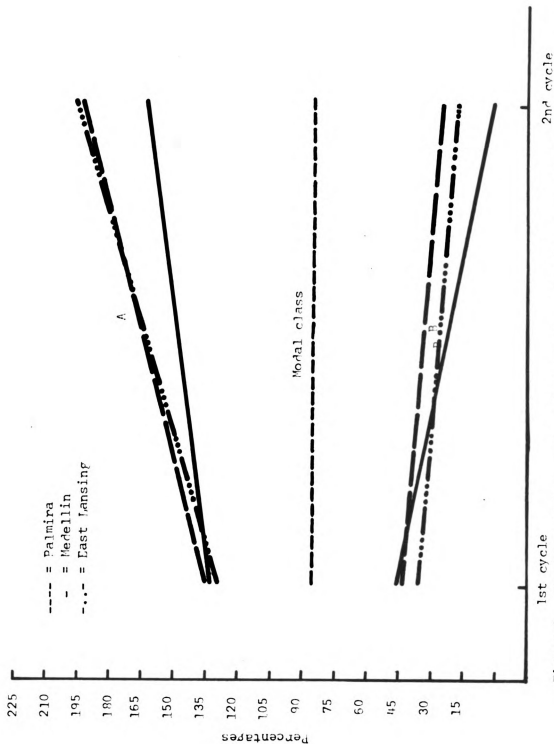
Figure 3. Response to two cycles of recurrent selection for high (A) and low (B) level of expression of number of pods per plant (Y), at Palmira, Medellin and East Lansing. Data are expressed as percentage of the modal class.

D. Number of Seeds Per Pod (Y)

Mean values of the selected families and t-tests between the two cycles of recurrent selection, for high (YA) and low (YB) number of seeds per pod at Palmira, Medellin and East Lansing are presented in Tables 4.1 and 4.2. Rates of progress between cycles in the three different locations are shown in Figure 4.

From the t-tests presented in Table 4.1 it may be seen that the differences between the two cycles for YA ranged from highly significant in East Lansing to no significance in Medellin. Palmira shows a difference between cycles significant at the 5 percent level.

Even though Medellin does not show a significant difference between cycles, a progress of 25 relative units for YA was obtained, as shown in Figure 4. In Palmira and East Lansing, 69 and 58 relative units of progress were observed.

Table 4.2 shows that a highly significant difference between cycles for the low level of expression of number of seeds per pod was obtained in Medellin. A significant difference at the 5 percent level was observed in Palmira and no significance was found at East Lansing.

Thirty five relative units of progress were obtained at Medellin, followed by Palmira with 21 and East Lansing with 4, as shown in Figure 4.

Table 4.1   t-tests and mean values of families selected for high
number of seeds per pod (YA), in two cycles of re-
current selection at Palmira, Medellin and East Lansing.
Data are expressed as percentage of the modal class.

| Locations | Values of 4 selected families | | t-values |
	1st cycle	2nd cycle	
Palmira	130.68	265.13	
	127.84	181.34	
	127.84	177.06	
	139.20	176.75	
Average	131.39	200.07	3.19*
Medellin	131.91	172.41	
	126.78	134.49	
	125.64	134.49	
	125.07	170.69	
Average	127.35	153.02	2.37
East Lansing	137.30	203.20	
	138.90	190.30	
	148.10	209.70	
	152.30	206.40	
Average	144.10	202.40	10.40**

*P < .05
**P < .01

Table 4.2 t-tests and mean values of families selected for low
number of seeds per pod (YB), in two cycles of re-
current selection at Palmira, Medellin and East Lansing.
Data are expressed as percentage of the modal class.

Locations	Values of 4 selected families		
	1st cycle	2nd cycle	t-values
Palmira	71.02	40.36	
	73.86	46.78	
	73.86	55.96	
	68.18	59.63	
Average	71.73	50.68	4.60*
Medellin	62.68	29.31	
	70.66	36.21	
	70.66	31.03	
	72.93	37.93	
Average	69.23	33.62	11.69**
East Lansing	48.16	54.83	
	52.37	41.93	
	53.95	51.61	
	59.47	48.38	
Average	53.49	49.18	1.19

*P <.05
**P <.01
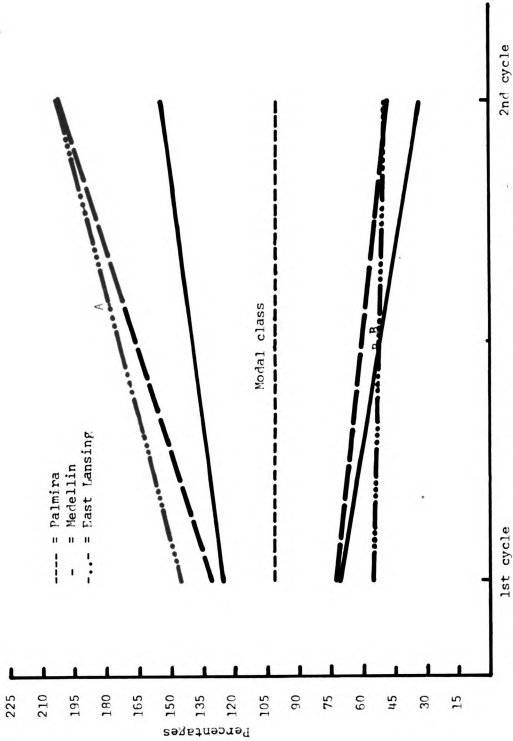
Figure 4. Response to two cycles of recurrent selection for high (A) and low level of expression of number of seeds per pod (Y), at Palmira, Medellin and East Lansing. Data are expressed as percentage of the modal class.

Tables 5.1 and 5.2 contain mean values of selected families and t-tests between 2 cycles of recurrent selection for high (ZA) and low (ZB) levels of expression of seed weight, at Palmira, Medellin and East Lansing. Figure 5 shows the progress made in the 2 cycles at the three different locations, for ZA and ZB.

From the t-values shown in Table 5.1 it may be seen that a highly significant difference between the 1st and the 2nd cycle of recurrent selection for ZA was obtained in East Lansing. No statistically significant difference was found either at Palmira or at Medellin. However, a progress of 58 relative units for ZA was achieved between the two cycles at Medellin; forty-eight relative units were obtained at East Lansing and four in Palmira.

In Table 5.2 it may be seen that significant differences at the 5 percent level between the two cycles for ZB were obtained at Medellin and East Lansing but differences were not significant at Palmira.

Figure 5 shows essentially parallel lines for selection gain at the three locations when selections were made for ZB. In each one of the locations eleven relative units of progress in the selected directions were obtained.

Table 5.1 t-tests and mean values of families selected for high
seed weight (ZA), in two cycles of recurrent selection
at Palmira, Medellin and East Lansing. Data are
expressed as percentage of the modal class.

| Locations | Value of 4 selected families | | |
	1st cycle	2nd cycle	t-values
Palmira	144.68	166.03	
	140.42	135.84	
	136.17	135.84	
	136.17	135.84	
Average	139.36	143.39	0.516
Medellin	165.99	326.67	
	149.79	180.00	
	141.70	160.00	
	141.70	166.67	
Average	149.79	208.39	1.27
East Lansing	126.40	181.30	
	130.00	181.30	
	132.90	184.40	
	142.60	178.10	
Average	132.90	181.30	13.05**

**P <.01

Table 5.2 t-tests, and mean values of families selected for low
seed weight (ZB) in two cycles of recurrent selection,
at Palmira, Medellin and East Lansing. Data are
expressed as percentage of the modal class.

Locations	Values of 4 selected families		t-values
	1st cycle	2nd cycle	
Palmira	63.82	45.28	
	72.34	60.37	
	68.08	60.37	
	72.34	64.15	
Average	69.14	57.54	2.20
Medellin	56.68	53.33	
	64.78	53.33	
	68.82	53.33	
	68.82	53.33	
Average	64.77	53.33	4.00*
East Lansing	58.23	46.87	
	60.29	53.12	
	63.82	50.00	
	65.00	50.00	
Average	61.83	49.99	5.13*

*$P < .05$
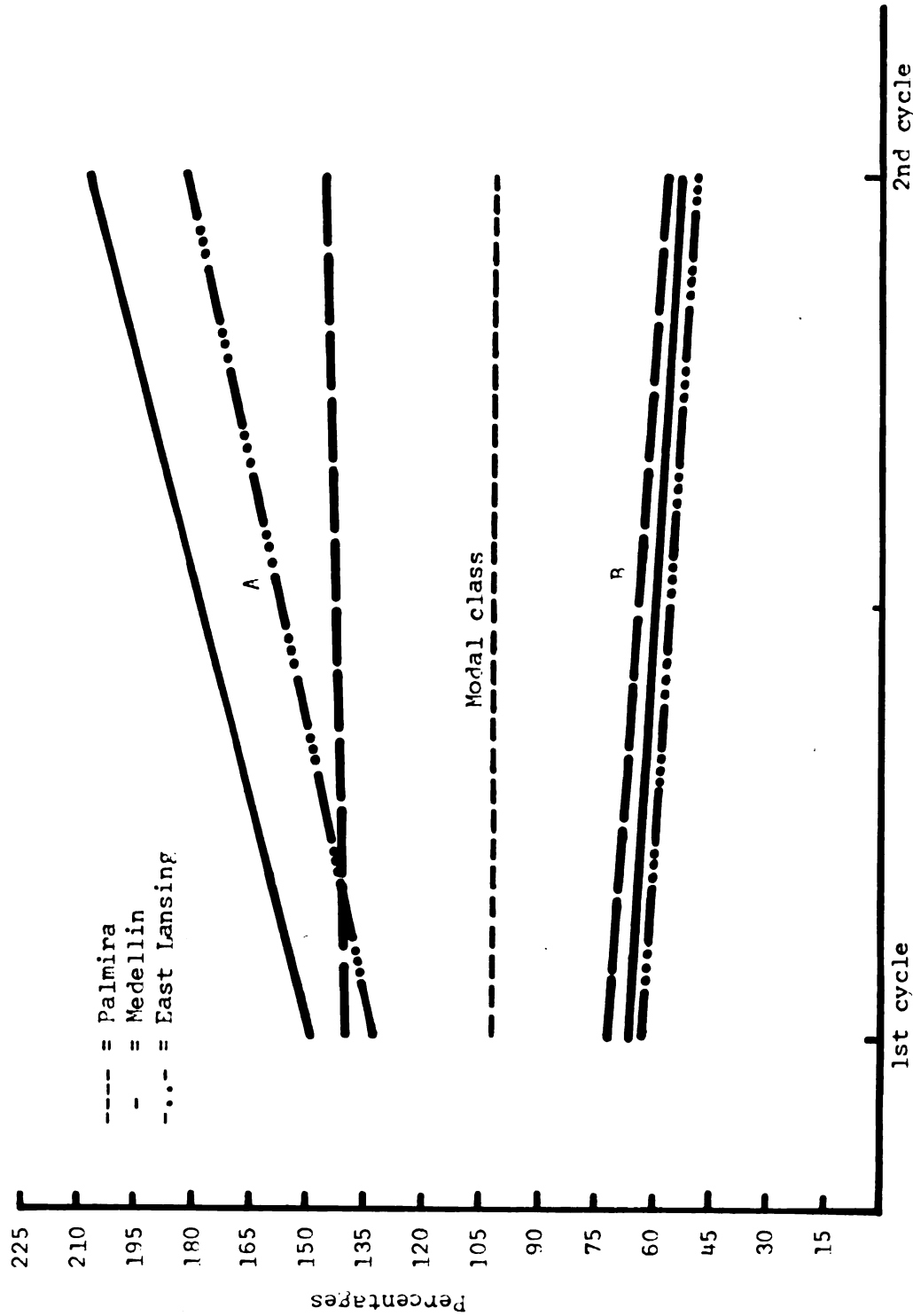
Figure 5. Response to two cycles of recurrent selection for high (A) and low (B) levels of expression of seed weight (%), at Palmira, Medellin and East Lansing. Data are expressed as percentage of the modal class.

---- = Palmira
— = Medellin
-..- = East Lansing

1st cycle   2nd cycle

Percentages

Modal class

A

B

F. Seed Yield (W)

Mean values of the selected families and t-tests between the two cycles of recurrent selection, for high (WA) and low (WB) levels of expression of seed yield are presented in Table 6. Figure 6 shows the response of selection for WA and WB at East Lansing between the two cycles and also the rate of progress of the individual yield components at high (A) and low (B) levels of expression.

From table 6 it appears that significant differences at the 5 percent level existed between the two cycles of recurrent selection for WA. In the case of WB no significant difference was found.

In Figure 6 it appears that even though 14 relative units of progress were obtained for WA and three for WB, these units were in the direction opposite to that for which they had been selected.

G. Discussion

A ceiling upon possible progress in straight pedigree selection is established by the genotype of the foundation plants. Recurrent selection breaks this ceiling inasmuch as cyclic selection and recombination increases the frequency of desirable genes and gene combinations in the population.

Table 6 t-tests and mean values of families selected for high
(WA) and low (WB) seed yield, in two cycles of re-
current selection at East Lansing. Data are expressed
as percentage of the modal class.

	East Lansing		
	Values of 4 selected families		
Level	1st cycle	2nd cycle	t-values
WA	150.45	145.49	
	155.54	142.09	
	156.58	142.99	
	164.04	140.66	
Average	156.65	142.81	4.64*
WB	78.70	60.83	
	44.20	42.03	
	46.40	41.85	
	49.72	87.40	
Average	54.75	58.03	0.244

*$P < .05$
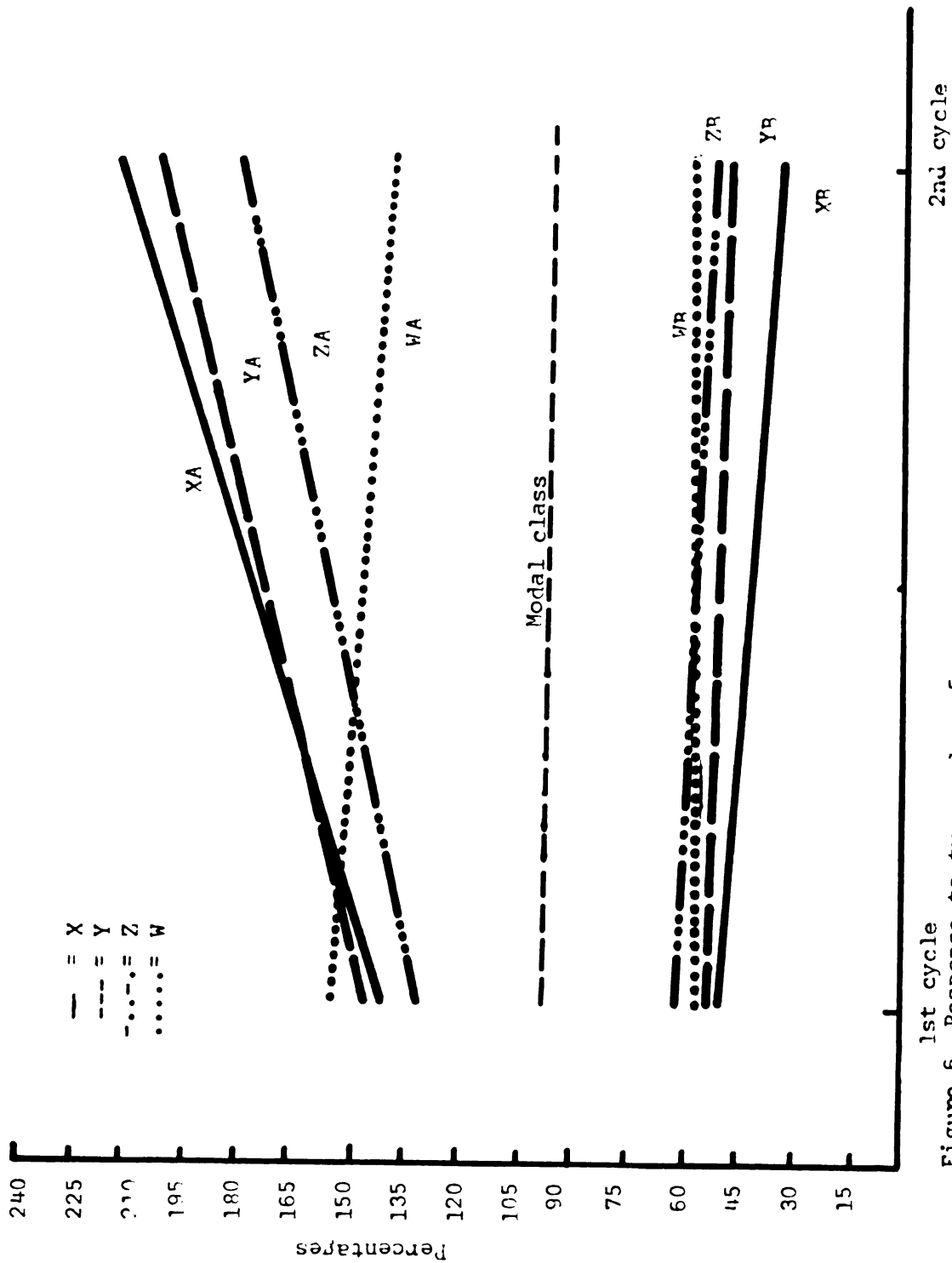
Figure 6. Response to two cycles of recurrent selection for high (A) and low (R) levels of expression of X, Y, Z and W at East Lansing, expressed as percentage of the modal class.

From the results shown in the preceding sections, it is clear that progress due to selection was made for each one of the components of both yield and leaf area. The rate of progress for each particular component, at either the high or low level of expression, was not the same at each location. Genes are expressed differently as the environment varies. Full expression of these genes could be obtained under certain environmental conditions, whereas under other conditions intermediate expression or almost complete suppression of their effects could be inferred.

Considering total leaf area components, namely, number of leaflets per plant (N) and leaflet size (S), it was seen in Figures 1 and 2 that more progress for NA was achieved in Medellin than in Palmira.

The opposite situation was true when selection was carried out for large leaflet size (SA); the gain in the latter was markedly higher in Palmira than in Medellin. This situation may be interpreted on the principle that through recurrent selection and recombination, genes favoring certain traits can be recovered in greater frequency at one location than at another for they are expressed more in one environment than in another.

There is also the possibility that the superior adaptiveness associated with the Algarrobo genotype at Medellin tends to be reflected in the kinds of plant characteristics that are selected under that environment. This might explain why selection for smaller leaflet size at Medellin was ineffective, the Algarrobo type, with

relatively large leaflets, being favored by natural selection forces over the Michelite type with relatively small leaflets.

The range of variability between low and high levels of N and S appears to be different at each one of the locations when selections were performed at the completion of the second cycle. While for N at Medellin the range goes from 46.06 to 245.65 (percent based on the modal class = 100%), the range for the same character at Palmira was from 44.52 to 180.43 (Figure 1).

These differences in realized gain from selection for two characteristics in two different environments can probably be accounted for by differential heritabilities of the traits selected for at Medellin and Palmira. Putting it another way, the first cycle selections for NA at Medellin produced upon intercrossing an array of genotypes some of which showed very high expression under the Medellin environment of the second cycle. Similar first cycle selections at Palmira either did not have the recombination potential or the new genotypes produced by intercrossing were less strongly expressed in the Palmira environment.

A similar situation to that discussed for leaf area prevails for yield components. From the results it is clear that greater progress for the high expression of number of pods per plant (XA) and number of seeds per pod (YA) was obtained at East Lansing and Palmira than at Medellin. However, for high level of seed weight (ZA) greater gain was achieved at Medellin than at either East Lansing or Palmira (Figures 3, 4, 5 - Tables 3.1, 4.1, 5.1).

Selection for the low expression of yield components resulted in more progress for XB and YB at Medellin than at East Lansing or Palmira (Figures 3, 4, 5 - Tables 3.2, 4.2, 5.2). For lower expression of seed weight (ZB) no differences among locations were detected.

Here again, genotypic-environmental interactions, and the association of the parental type at certain locations seems to be true. The Michelite type has been recovered more often than expected at East Lansing, as suggested by response in higher number of pods per plant and seeds per pod. On the contrary, at Medellin the Algarrobo type seems to be predominant as suggested by the heavier seeds recovered in that location. Palmira behaves as intermediate between the other two locations, even though more progress was observed for higher expressions of number of pods per plant and number of seeds per pod, than for seed weight.

These findings demonstrate that selection directed toward increasing the level of certain components at each location is worthwhile. Much more progress could be made in yield if, for instance, at East Lansing and Palmira, selection were directed more toward increasing X and Y than Z, the opposite being true at Medellin. Similar reasoning could be applied to leaf area components at the two locations in Colombia.

Thus far, selection for yield components has been discussed and shown to be effective. But what happens when selecting for

yield itself? From Table 6 and Figure 6, it may be seen that
even though progress was made for yield it was in the "negative"
direction; that is, when selections were made for high seed yield
level (WA), instead of increasing, yield actually decreased; the
opposite situation arose when selecting for low yield (WB), -
an increase was noticed. Although the comparison between the
two cycles was significant at the 5 percent level for WA, only
14 relative units of "negative" progress were obtained and for
WB only 3 relative units.

Figure 6 shows graphically the response of selection for
yield components, namely X, Y and Z, as compared to selection
for yield itself (East Lansing). Great progress was obtained
for each one of the components in both directions - high and
low levels of expression. However, as was discussed, "negative"
progress was observed for yield. This is not to say that select-
ing for high yield will always render lower yields. It was true
for this particular cross at this particular location, it is
also necessary to recall that in Figure 6 the values are expressed
as percentage of the modal class in both cycles, and also that the
modal class changed slightly from the 1st to the 2nd cycle.

Table 7 shows average values of yield in grams per plant when
selections were made for X, Y, Z and W at high (A) and low (B)
levels. It is interesting to note from this table that actual
seed yield was higher when selections were made for XA and YA than
when selection was for WA, being in the case of ZA more or less

the same as WA. The same situation prevails when selections
were performed for low levels of yield components and seed yield
itself; lower yield values were obtained for XB and YB than WB,
being in the case of ZB a little higher than WB. However, these
differences were not of sufficient magnitude to be regarded as
important. Practically speaking all values are the same.
This means that progress for yield was not really made. Progress
in the values of individual components were obtained, but the
progress in one component was at the expense of another or other
components, giving through their multiplicative interaction more
or less the same result as far as seed yield was concerned. This
implies negative correlations among yield components, a discussion
of which will be postponed for a later section of this thesis.

Yield is greatly modified by environmental factors; however,
it shows a kind of homeostatic stability to offset the force of
selection, in any direction, high or low, without appreciable
changes in magnitude. This homeostatic stability of seed yield
seems also to be true, when selection of individual components
was performed.

In some cases, and especially at Medellin, non-significant
differences between means were obtained when comparing the two
cycles of recurrent selection, even though the progress
measured in relative units showed patently that progress was made;
the explanation lies in the fact that large variances were ob-
tained, resulting in a non-significant t-test. The amount of the

variance could be very large in magnitude even if only a single family out of four exhibits a different value. This is the case, for example, shown in Table 5.1 at Medellin. The t-test shows a non-significant value; however, it may be seen that the first family in each one of the cycles shows a much higher value than the remaining three. If a t-test is performed just among the three families a highly significant difference is obtained.

Table 7. Average seed yield in grams per plant, for X, Y, Z and W. Selected families at the end of the 2nd cycle of recurrent selection, in two levels, high and low, at East Lansing.

	High Level	Low Level
Seed Yield (W)	23.92	9.72
Number of pods per plant (X)	26.00	5.56
Number of seeds per pod (Y)	26.66	6.06
Seed weight (Z)	18.31	10,69

II. Compensation Among Yield Components

In the preceding section of this thesis the response to
selection for individual yield components and yield itself
was discussed. This section will be concerned with the
effects that selection for a given component has upon the
non-selected components, for example, the effect that
selection for number of pods per plant (X) has upon the number
of seeds per pod (Y) and the seed weight (Z) in the same
families.

This situation is graphically presented for the first
and second cycles of recurrent selection at three locations,
Palmira, Medellin and East Lansing, in percentages based on
the appropriate modal class as 100 percent (Figures 7, 8,
9, 10, 11, 12).

A. First Cycle

Palmira

Figure 7 shows the effect of selection for each one of the
yield components upon the non-selected ones, at Palmira in the
first cycle of recurrent selection. Families selected for XA
reached an average of 150 percent, that is 50 relative units
above the modal class, while Y for the same set of families is
near the 100% point, and Z 15 units lower than the modal class.
Selections for XB with an average of 58 percent (42 relative
units below the modal class) exhibit a Y value of 85% and a Z
value of 108%. It should be noted that the slopes of the lines

representing the relative effects on sequential components Y and Z, by selection for X, are generally downward for the XA selections and upward for the XB selections.

Selection for YA and YB present a pattern similar to that of selection for X. The slope of lines converging at X, though near the average, shows a negative relationship with Y; this effect is more pronounced for unselected Z.

Selection for ZA depressed the values of X and Y, bringing them down 10 and 18 relative units respectively below the modal class; on the contrary, selection for ZB resulted in increased values of Y and X, 8 and 9 relative units over the 100 percent.

It is interesting to notice that the two X lines for selected levels of expression (XA and XB) cross at certain points; the same thing is true for YA and YB, as well as for ZA and ZB selections, suggesting particularly that Z is often involved in these component adjustments.

Relationships in the first cycle of recurrent selection among selected yield components and non-selected ones at Medellin and East Lansing are presented in Figures 8 and 9 respectively.

Patterns of variation similar to those obtained at Palmira were found at Medellin and East Lansing. The relationship between the selected and unselected components was essentially the same, showing negative associations; however, if one of the unselected characters goes too far in a direction opposite to the selected one, the third component varies directly as the selected one,
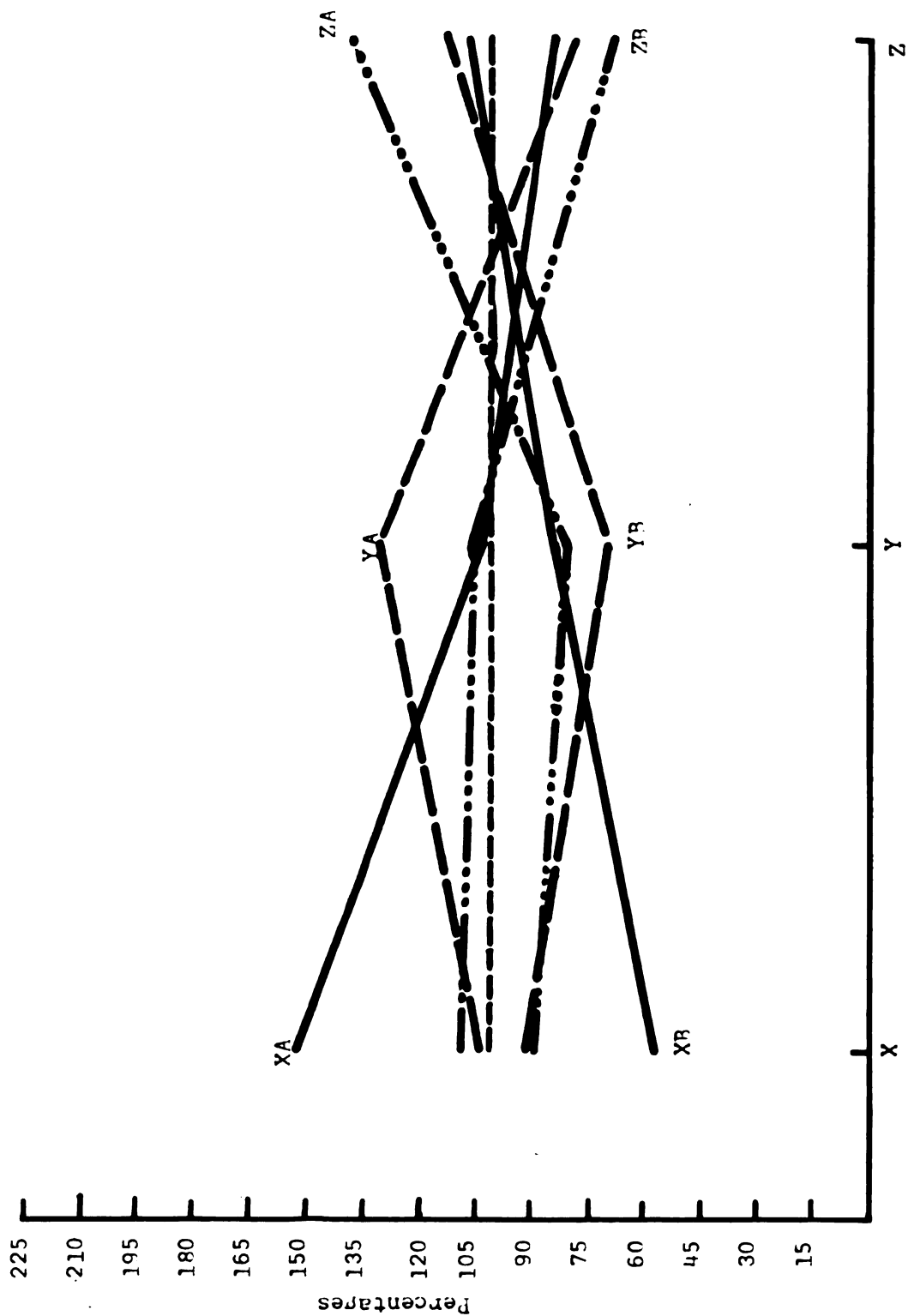
Figure 7. Effects of selection for either X, Y or Z individually upon relative values of the other two components. Data are obtained from 1st cycle of selection at Palmira and expressed in percentages on the nodal class.

stabilizing in this manner the final product yield.

This pattern of relational symmetry and reversion toward the modal values for the non-selected components is typical of all locations.

B - Second Cycle

Figures 10, 11 and 12 show graphically the effect of selection upon selected and non-selected yield components, at Palmira, Medellin and East Lansing, respectively.

The second cycle results in patterns of variation similar to the first one. The compensation among the yield components is particularly clear in the second cycle. Because of the great progress made by selection for individual components, the negative relationships with the unselected ones were exaggerated, as indicated by the slope of the lines, which are much steeper than in the first cycle.

The reversion of the non-selected components toward the modal class is very clear, showing a pattern of relational symmetry which is practically the same at all locations.
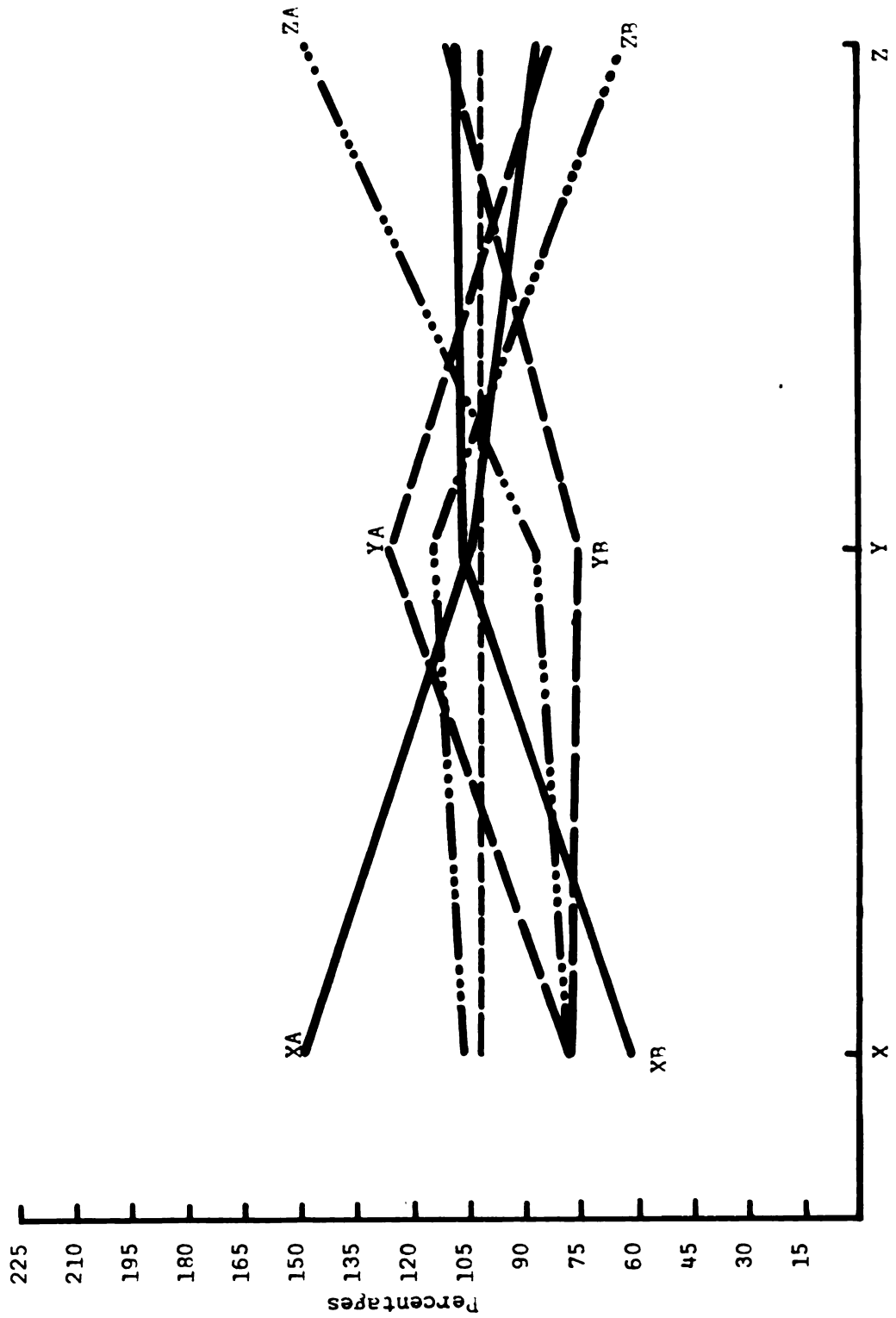
Figure 8. Effects of selection for either X, Y or Z individually upon relative values of the other two components. Data are obtained from 1st cycle of selection at Medellin and expressed in percentages on the modal class.
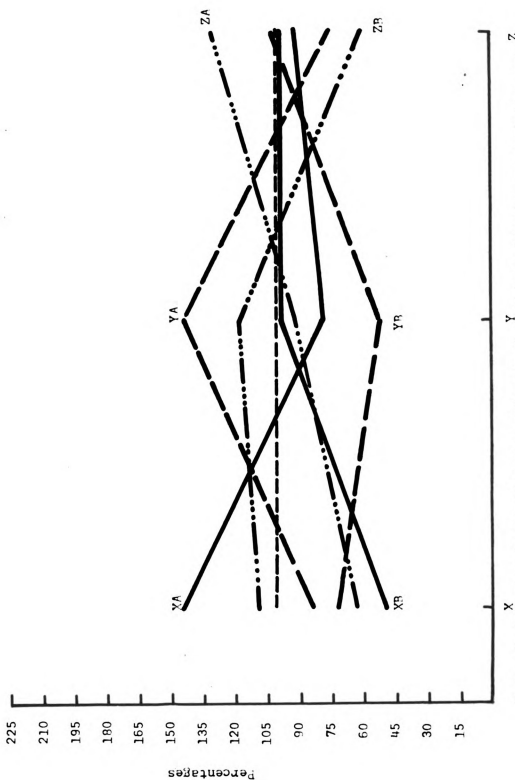
Figure 9. Effects of selection for either X, Y or Z individually upon relative values of the other two components. Data are obtained from 1st cycle of selection at East Lansing and expressed in percentages on the modal class.

Figure 10. Effects of selection for either X, Y or Z individually upon relative values of the other two components. Data are obtained from 2nd cycle of selection at Palmira and expressed in percentages on the modal class.
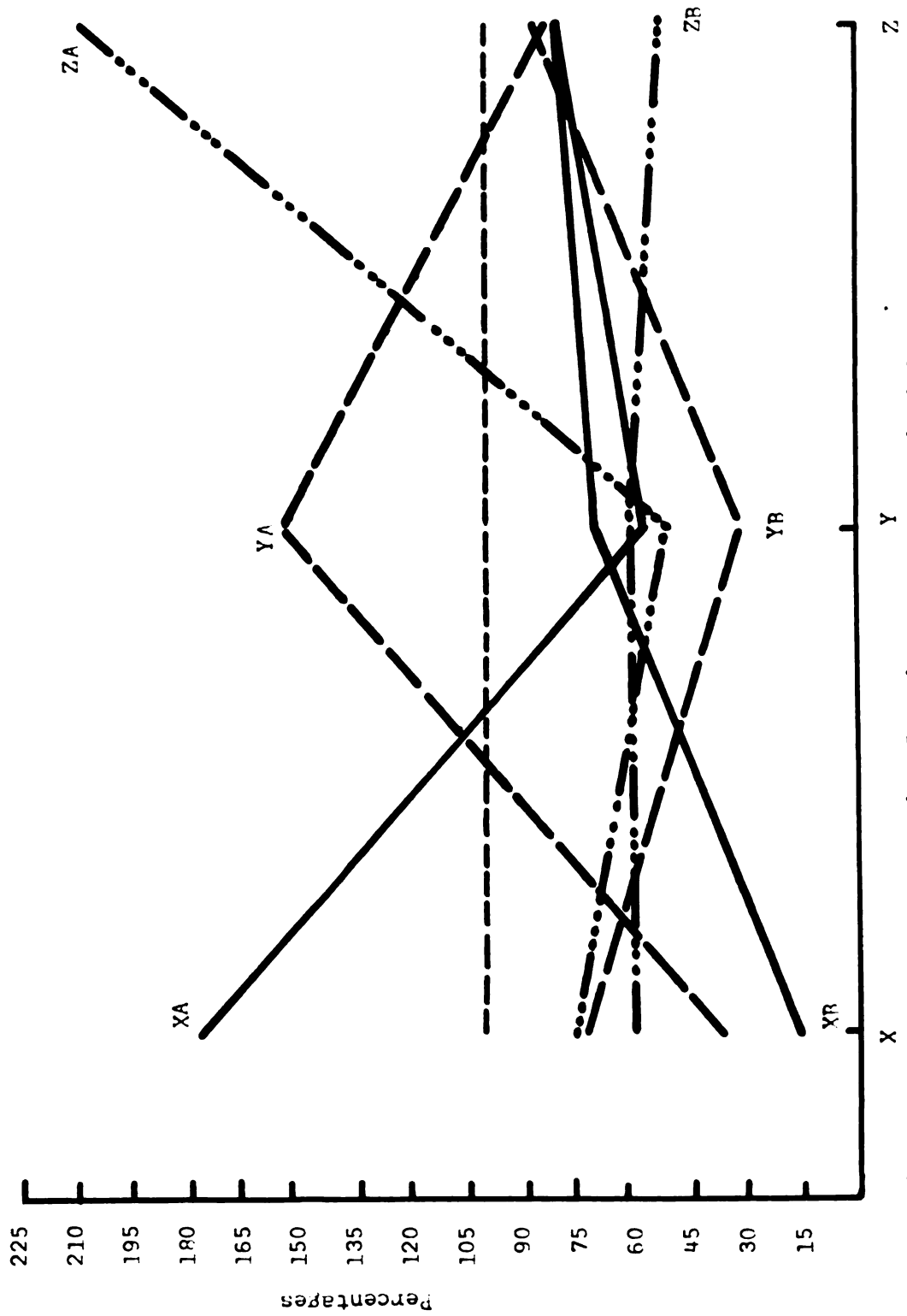
Figure 11. Effects of selection for either X, Y and Z individually upon relative values of the other two components. Data are obtained from the 2nd cycle of selection at Medellin and expressed in percentages on the nodal class.
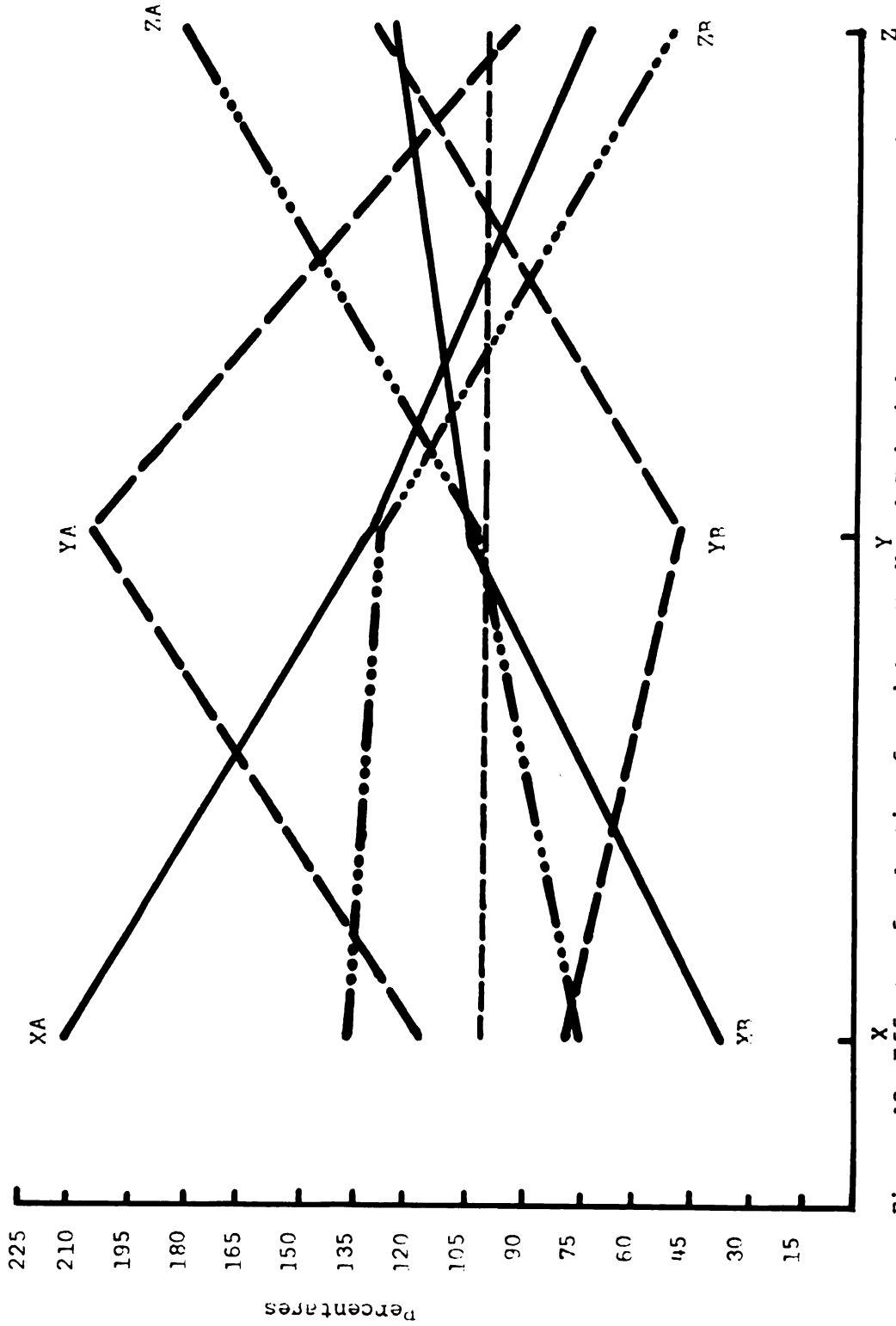
Figure 12. Effects of selection for either X, Y and Z individual upon relative values of the other two components. Data are obtained from 2nd cycle of selection at Fast Lansing and expressed in percentages on the modal class.

C. Correlation Coefficients

In the preceding sections the relationship among selected and unselected yield components was presented and discussed. Correlation coefficients were not calculated inasmuch as only four families were selected for each character at each level, therefore, the number of pairs being too few, the expected error would have been of high magnitude.

Phenotypic correlation coefficients for 36 families selected for yield components at each location, Palmira, Medellin and East Lansing, are presented in Tables 8 and 9 for the first and the second cycle of recurrent selection, respectively.

Considering the first cycle, it may be seen in Table 8 that X and Y are positively correlated at all locations, though none reached the significance level. The association XZ was negative and significantly different from zero at the .05 level in Palmira and Medellin and near significance at East Lansing. There was significant negative correlation between Y and Z at the three locations.

X, Y and Z are positively correlated with yield at all locations except for East Lansing where ZW is negative although of very low magnitude. X is the component which shows most association with W. It is interesting to notice that in Medellin the magnitude of association of XW, even though is highly

significantly different from zero, is lower than in Palmira or

East Lansing. On the contrary the correlation coefficient

between Z and W at Medellin is positive and significant, being

not different from zero at the other two locations.

Table 8. Simple correlation coefficients of families selected
for yield and its components, in the first cycle of
recurrent selection at Palmira, Medellin and East
Lansing.

Comparison	Locations		
	Palmira	Medellin	East Lansing
XY	.265	.189	.021
XZ	-.347*	-.366*	-.305
XW	.832**	.648**	.737**
YZ	-.588**	-.534**	-.401*
YW	.467**	.198	.428**
ZW	.016	.393*	-.003

Table 9. Simple correlation coefficients of families selected
for yield and its components, in the second cycle of
recurrent selection, at Palmira, Medellin and East
Lansing.

Comparison	Locations		
	Palmira	Medellin	East Lansing
XY	-.207	-.246	-.137
XZ	.287	.140	-.334*
XW	.848**	.596**	.803**
YZ	-.463**	-.016	-.461**
YW	.162	.250	.495**
ZW	.221	.662**	-.018

D. Discussion

From the results presented in the preceding sections there is apparent a similar pattern of variation with respect to the behavior of unselected yield components at the three locations under study during the first cycle of selection. Progress for selected components was somewhat different especially between the Colombian locations and East Lansing. While in the latter location greater gain was obtained for X and Y than for Z, in Palmira and Medellin more progress was achieved for Z and X, especially for Z at Medellin. The unselected components exhibit negative relationships with the selected ones, the magnitude of the association depending upon the response to selection.

The second cycle of recurrent selection presents some aspects similar to the first cycle as far as negative association among selected and non-selected yield components is concerned. However, as may be seen from Figures 10, 11 and 12, the slope of the lines is steeper than in the first cycle. This results from the fact that progress in selection for yield components was greater in the second cycle, and in the same manner the degree of compensatory relationship between selected and non-selected components increased in magnitude. For both cycles if one of the unselected components reverts too far in a direction

opposite to the selected one, the third component varies in the same direction as the selected one, stabilizing in this manner the final product, yield. In general, this pattern of compensation among components holds true at all locations. To illustrate this situation, let us take as an example the case of selection for XA at Medellin and East Lansing during the second cycle (Figures 11, 12). It can be seen that in the former case a high negative relationship exists between selected XA and unselected Y, whereupon Z shows positive association with XA, going up from the mean value of Y; at the latter location XA exhibits a negative relationship with Y but not as strong as in Medellin, therefore, the line continues downward to a lower value of Z, giving negative associations with both unselected components Y and Z. Another example of this harmonic balance among yield components is furnished by ZA selections at Palmira (Figure 10), where the value of Y was the lowest one, (with the exception of YB selections), suggesting strong negative association with ZA; however, the un-selected X shows much higher value with respect to Y, having a positive association with ZA. A similar situation prevails for ZB selections although it is not as striking as in the case of ZA. These examples and the fact that in most cases the trend lines connecting values of non-selected characters at the high and low levels of expression, cross over once or even twice at different points, tends definitely to support the hypothesis that yield

exhibits homeostatic stability, implying that no greater changes could be obtained either selecting for yield itself or independently for its components because of compensatory mechanisms existing in the plant.

The idea of negative associations among components of yield is supported by the phenotypic correlations presented in Tables 8 and 9. These correlations were expected to be in that direction, but the point of interest lies in the nature and course of this association.

Assuming that the correlation coefficients shown in this study are of genetic origin, and having in mind that X, Y and Z evidenced positive relationship with W, does it really mean that yield and its components are controlled by the same genetic system? This is not necessarily true. Genetic correlations may be originated between different characteristics due to genetic linkage, or pleiotropic effects; correlation will also result when characters share a common pool of metabolic resources for their development, generated by a given set of genes.

This seems to be the case with respect to yield and its components in the present study in beans. For if it were otherwise then changes of environment, or changes in mean values of components due to selection, would not be reflected in the direction of the association, shifting it from positive to zero or to negative or vice versa. Opposite findings should demonstrate

that more or less independent genetic system condition each of the components.

The correlation coefficients observed in the first cycle (Table 8) are different from those of the second cycle (Table 9). Although the degree of association between X and Y is not significantly different than zero in both cycles, is interesting to note that the correlation coefficients were positve in the first cycle and became negative after the second cycle of selection at all locations. A similar situation prevails between X and Z; whereas in the first cycle the correlations are negative at the three locations, being significantly different from zero at Palmira and Medellin, in the second cycle they became positive at the Colombian locations. However, in East Lansing, the association is still negative and significant. At Medellin the correlation between Y and Z is highly significantly different from zero in the first cycle, but becomes zero after the second cycle of selection. These findings demonstrate that the effect of selection and/or environment can change the degree of association among components.

The correlations coefficients presented agreed completely with the results shown in Figures 7 to 12, already discussed. The compensatory mechanisms among the yield components are able to change the direction of the association between them when selection pressure is applied to an individual component, giving rise to changes in signs of the correlation coefficients.

Not only selection can change the direction and magnitude

of the association between yield components in beans; under

greenhouse conditions Montoya and Adams (8) were able to in-

crease the number of seeds per pod and seed size by removing half

of the pods in navy beans. Archibong (1) showed that in beans

the correlation between components could be strong and negative

when they are planted at high densities but they can become

zero or even positive when the plants are spaced greatly.

Rendel (10) studied the number of scutellar and abdominal

bristles in Drosophila melanogaster. He found positive corre-

lations between the two characters in unselected stocks. The

correlation was negative in selected genotypes but it became

positive with further selection. He explains these facts by

showing that total resources for making bristles can be varied,

and the proportion allocated to the two kinds of bristles can

also be varied. The former variation results in positive, the

latter in negative correlations.

Changes in the direction of the correlations similar to

those found by Rendel (op. cit.) occurred in some cases between

unselected and selected families in the present investigation.

As an example from the location at Medellin, a comparison of

correlations between the 768 F_3 unselected families and the 36

selected ones in the second cycle of recurrent selection is pre-

sented in Table 10. From this table it may be seen that the

degree of association between number of pods per plant (X) and number of seeds per pod (Y), which exhibits a positive and significant correlation coefficient in the unselected stock, became negative and non-significant in the selected one. The magnitude of the degree of association also changed; as in the case of Y and Z, the correlation coefficient is negative and highly significantly different from zero among the non-selected progenies but is not significant among the selected families. Also the magnitude of influence of Z upon W becomes higher after selection, increasing the correlation coefficient from .36 to .66, although both are significant at the 1 percent level.

The results of the present investigations, coupled with the findings of other authors, strongly suggest that the correlations among yield components are not truly genetic in the sense of linkage or pleiotropism inasmuch as they could be changed by selection pressure and environmental conditions. It also furnishes evidence indicating that mainly independent genetic systems are controlling each one of the yield components in beans. The idea of very close linkage among the genetic systems of the components is also precluded, because the changes in the direction of the correlation coefficients are found in much higher proportion than expected from crossing over alone.

Table 10. Simple correlation coefficients for yield and its
components, for 768 unselected and 36 selected
families during the second cycle of recurrent
selection, at Medellin.

Comparison	Unselected Families	Selected Families
XY	.109*	-.246
XZ	-.005.	.140
XW	.731**	.596**
YZ	-.178**	-.016..
YW	.348**	.250
ZW	.362**	.662**

Calculated "genetic" correlations could arise in different

ways as was stated before. One way to obtain them could be when

characters controlled by essentially different genetic systems

share a common pool of metabolic resources for their development,

the genetic regulation of the amount of these resources to be

apportioned to the component characters may itself be the most

acceptable hypothesis to account for the component relationships

under consideration in the case of beans.

In the discussion of this hypothesis to follow, reference

will be made to the following symbols: A, those genes condition-

ing high values of any of the yield components; B, those genes for

low values of yield components; R, genes or sets of genes con-

trolling metabolic resources; and U, the amount of metabolic

resources available during the time of yield component develop-
ment. It is also implied that the components are sufficiently
flexible in their development to be responsive to the amount of
resources available, except when limited by genotype.

This hypothesis is stated briefly as follows: There is a
common pool of metabolic resources U whose amount is controlled
by genes R; this pool should be shared by X, Y and Z. The dis-
tribution of U among yield components depends on an interaction
between the genotype of each one of the components and one or
more of the R genes. This interaction which takes the form of
an induction or "turning on" process occurs at certain stages
prior to floral development. At that time the genes controlling
X, Y and Z are activated by interaction with R genes; the share
that each component receives depends on this interaction. If
by selection pressure A genes for high level of expression have
been accumulated for a given character, for example, this
character would receive proportionally greater amounts of U than
X and Y. The opposite result with the same mechanism operating
would be true if selection were for B genes conditioning a low
expression of Z, thereby generating negative correlations,
correlations that are at the developmental or morphological level
rather than at the genetic level.

An alternative hypothesis would also postulate a common pool
of metabolic resources, these resources to be shared by X, Y and Z.

Yield components follow a sequential pattern of development,
and each one has its own genetic basis. When selection is for
a high level of expression of X, A genes are accumulated and
the character, number of pods, would receive a greater share
from the common pool. However, if a proportionately greater
share of the resources were used in producing high X, a proportion-
ately lesser amount would be available for producing high Y-values,
or possible Z values, which follow X in the developmental sequence.
On this account, negative correlations might be expected
between X and Y, possibly between X and Z.

If selection is for low values of X, then there are more
resources available for Y and Z, so once again negative relation-
ships might be induced. For this pattern of cause-effect
relationship to prevail, however, it is necessary to assume a
flexibility of development of Y and Z particularly, such that
they are affected in their development not only by the underlying
genotypes but by the amount of growth resources available.

When selection is for high values of a component such as Z,
which follows X and Y in the sequence, how might it be effective,
under this alternative hypothesis? One explanation could be
that A-genes for Z could only be expressed when resources U are
plentiful, which implies that ZA genes would be selected for most
readily in a background of XB genes and YB genes, backgrounds which
utilized a relatively minor share of resources, ahead of utilization
by Z. This is a case of adaptive compensation, referred to by

Stebbins (11), and which in this instance, results once more in negative correlations.

Highly significant correlations were observed between each one of the yield components and the total seed yield per plant (W), as was expected since seed yield per plant is a product of the three components, namely: number of pods per plant (X); number of seeds per pod (Y); and average weight of the seed (Z).

Selection for high levels of any one of the components should increase yield. From results presented here, even though selection progress was obtained separately for each one of the components, the unselected components exhibited almost counter-balancing lower values, leaving the final product yield practically unchanged. This is not to say that yield through the enhancement of components can not be increased. By artificial means, application of fertilizers, proper space-planting, cultural practices, etc., the pool of metabolic resources could be augmented. By these means, along with selection of A genes for each one of the components, the possibility of maximizing yield may be realized.

At the present it seems to be worthwhile to select for two components at the same time instead of one. Moreover, the selection pressure ought not to be very strong, in order to avoid within-plant competition for resources and hence negative associations. In Palmira and East Lansing, simultaneous selection for X and Y seems to be valuable. In Medellin, selection for X and Z would be much better.

However, by increasing two of the components even at the expense of stronger negative correlations with the third one, yield was also increased. A good example is furnished by the results at Palmira during the 2 cycles of recurrent selection. One family of the modal class selection during the first cycle has the following average values per plant: X equals 13.1, Y equals 3.0, Z equals 0.33 and W equals 13.0. In the second cycle one of the families selected for high X shows X equals 38.3, Y equals 3.9, Z equals 0.24, and W equals 35.9. Yield was increased almost 3 times by selecting X and involuntarily also Y. However, the value of Z went down, hence increasing the magnitude of the negative correlation.

As a practical application of the results obtained in this thesis it appears that in order to increase yield at Palmira and East Lansing selections for X and Y should be made at the same time. In Medellin joint selections for X and Z would be advisable. This recommendation seems to be true at least for this particular cross. The greater progress in Z at Medellin might be related to the natural superiority of the Algarrobo type, the same thing being true for the Michelite type at East Lansing. Neither type seems to be preferentially selected at Palmira.

III. Path Coefficients Analyses

Seed yield in beans is a product of number of pods per
plant (X), number of seeds per pod (Y), and average seed
weight (Z); thus the variation in yield depends on the
variation of the components; besides that, the variation of
the components depends on several other factors among which
are number of leaves per plant (N), and size of the leaves
(S).

Correlation coefficients show the degree of association
between two variables but they provide no information concern-
ing the dependence of one upon the other. When the direction
of this dependence is known, as in the case of yield components,
the correlation coefficients can be used in path coefficient
analyses to obtain information on the magnitude of direct and
indirect effects of the components upon more complex traits.

Two path analyses were made in this study. The first one
was to get information of the effects of number of pods per plant,
number of seeds per pod, and seed weight upon yield. The second
one was conducted in order to obtain some knowledge about the
effect of number and size of leaves upon the yield components
and through them to the seed yield.

Figure 13 shows the path diagram for factors influencing yield.
Direct effects are represented by single-arrowed lines and the

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correlation between two variables by double-arrowed lines. The correlation coefficients are broken down into direct and indirect effects and this relationship may be expressed as follows:

$$r_{XW} = P_{XW} + r_{XY} P_{YW} + r_{XZ} P_{ZW}$$

$$r_{YW} = r_{XY} P_{XW} + P_{YW} + r_{YZ} P_{ZW}$$

$$r_{ZW} = r_{XZ} P_{XW} + r_{YZ} P_{YW} + P_{ZW}$$

where r is the correlation coefficient between two variables, P is the path coefficient or direct effect, and r·P is the measure of the indirect effects.

The path coefficients were obtained by solving the correlation matrix by the use of determinants. To illustrate this with an example, the path coefficient between number of pods per plant (X), and seed yield (W), was obtained in the following way:

$$P_{XW} = \dfrac{\begin{array}{ccc} r_{WX} & r_{XY} & r_{XZ} \\ r_{WY} & r_{YY} & r_{YZ} \\ r_{WZ} & r_{ZY} & r_{ZZ} \end{array}}{\begin{array}{ccc} r_{XX} & r_{XY} & r_{XZ} \\ r_{XY} & r_{YY} & r_{YZ} \\ r_{XZ} & r_{ZY} & r_{ZZ} \end{array}}$$

$$P_{XW} = \frac{(r_{XW}\cdot 1\cdot 1) + (r_{WY}\cdot r_{ZY}\cdot r_{XZ}) + (r_{WZ}\cdot r_{XY}\cdot r_{YZ}) - (r_{WZ}\cdot 1\cdot r_{XZ})}{(1\cdot 1\cdot 1) + (r_{XY}\cdot r_{ZY}\cdot r_{XZ}) + (r_{XZ}\cdot r_{XY}\cdot r_{YZ}) - (r_{XZ}\cdot 1\cdot r_{XZ})}$$

$$\frac{-(r_{WY}\cdot r_{XY}\cdot 1) - (r_{WX}\cdot r_{YZ}\cdot r_{YZ})}{-(r_{XY}\cdot r_{XY}\cdot 1) + (1\cdot r_{YZ}\cdot r_{YZ})}$$

In a similar manner the path coefficients between Y and W, P_{YW}, and between Z and W, P_{ZW} are obtained; replacing Y for W in the second column of the numerator of the c-matrix and Z for W in the third column P_{YW} and P_{ZW} respectively are obtained. The
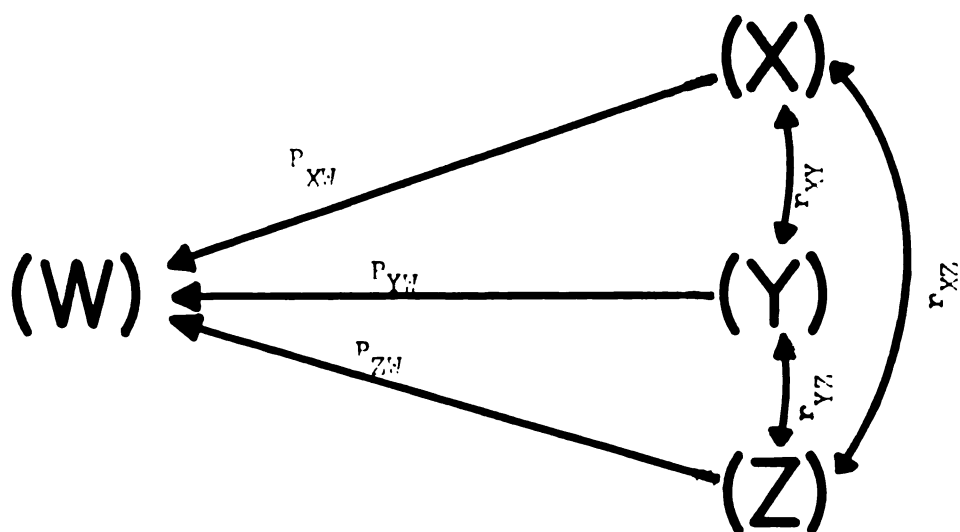
W = Total seed yield
X = Number of pods per plant
Y = Number of seeds per pod
Z = Seed weight
P = Path coefficient
r = Correlation coefficient

Figure 13. Direct effects and associations of components
determining yield.
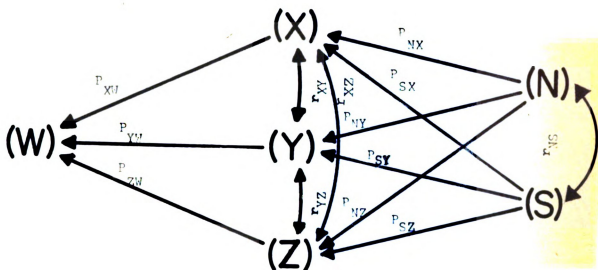
W = Total seed yield
X = Number of pods per plant
Y = Number of seeds per pod
Z = Seed weight
N = Number of leaflets per plant
S = Size of one leaflet
P = Path coefficient
r = Correlation coefficient

Figure 14. Direct effects and associations of components
of yield and factors influencing the components.

denominator was the same in all cases.

The diagram presented in Figure 14 shows the path coeffi-
cients and correlations between yield and its components, X,
Y and Z and also the direct effects of number of leaflets N
and size of the leaflets S upon the yield components.

The relationship between correlations and path coefficients
for N and S upon yield components are expressed in the following
equations:

$$r_{NX} = P_{NX} + r_{NS} \, P_{SX}$$
$$r_{SX} = P_{SX} + r_{NS} \, P_{NX}$$
$$r_{NY} = P_{NY} + r_{NS} \, P_{SY}$$
$$r_{SY} = P_{SY} + r_{NS} \, P_{NY}$$
$$r_{NZ} = P_{NZ} + r_{NS} \, P_{SZ}$$
$$r_{SZ} = P_{SZ} + r_{NS} \, P_{NZ}$$

Table 11. Simple correlation coefficients for yield and its
components, in families selected for X, Y, and Z
at high (A), intermediate (M) and low (B) level of
expression, at Palmira, Medellin and East Lansing
during the first cycle of recurrent selection.

Comparison	Selected-X	Selected-Y	Selected-Z
XY	-.218	-.168	-.298
XZ	.102	.277	-.134
YW	.888**	.852**	.793**
YZ	-.219	-.457**	-.420*
YW	-.098	.496**	.389*
ZW	.476**	.309	.377*

*   P < .05

** P < .01

Table 12. Simple correlation coefficients for yield and its
components, in families selected for X, Y, and Z
at high (A), intermediate (M) and low (B) level
of expression at Palmira, Medellin and East
Lansing, during the second cycle of selection.

Comparison	Selected-X	Selected-Y	Selected-Z
XY	-.263	-.322	-.177
XZ	-.142	-.196	-.185
XW	.925**	.898**	.863**
YZ	-.379*	-.412*	-.388*
YW	.401*	.468**	.358*
ZW	.075	.193	.355*

* P < .05

** P < .01

Table 13. Simple correlation coefficients for N and S,
yield and its components, in families selected
for N and S at high (A), intermediate (M) and
low (B) level of expression, at Palmira and
Medellin during the first cycle of recurrent
selection.

Comparison	Selected-N	Selected-S
NS	-.148	-.194
NX	.606**	.743**
NY	.123	.100
NZ	-.190	-.280
NW	.525**	.721**
SX	-.234	-.077
SY	.144	.072
SZ	.519**	.521**
SW	-.030	.108
XY	.366	-.010
XZ	-.517**	-.342
XW	.913**	.931**
YZ	-.444*	-.297
YW	.534**	.136
ZW	-.283	-.099

* P < .05

** P < .01

The relationships between correlations and path coefficients for X, Y, and Z upon W are the same as those described for the previous case.

Table 11 shows correlation coefficients for yield and its components in sets of 36 selected families for each one of the components X, Y, and Z, at the high, intermediate, and low levels of expression at Palmira, Medellin, and East Lansing for the first cycle of selection. Similar sets of correlations for the second cycle are presented in Table 12. The correlations presented in Tables 11 and 12 show a pattern similar to those in the preceding sections of this thesis.

Estimates of the correlations between number (N) and size of leaflets (S), and yield and its components are presented in Table 13. These correlations were calculated from 24 families selected for N, and 24 for S, at the high, intermediate and low levels of expression, during the first cycle of selection at Palmira and Medellin.

Similar patterns of correlation are exhibited by families selected for N as well as those selected for S. Estimates involving number of leaflets and size of leaflets are negative although of low magnitude. This type of association between the components of total leaf area seems to be at the developmental or morphological level rather than at the genetic level, as was clearly demonstrated by Duarte and Adams (3).

The highly significant correlation between number of leaf-
lets (N) and number of pods (X), and between N and seed yield W,
suggests that yield is greatly influenced by number of leaflets
through number of pods which also show a high correlation with
yield. Seed size (Z) seems to be greatly influenced by size of
the leaflets (S). However, the correlation of the latter with
yield is not significantly different than zero, the same being
true for Z which shows a non-significant negative association
with yield.

Associations of low magnitude are observed between number
of leaflets (N) and number of seeds per pod (Y), and N and Z.
The same pattern prevails for correlations between S and X and
S and Y.

Table 14. Path coefficient analysis of the influence of X, Y and Z upon yield (W), in families selected for X at all levels, A, M, and B, at Palmira, Medellin and East Lansing in the first cycle of selection.

Type of effect	Coefficient
Effect of number of pods per plant (X)	
Direct effect (P_{XW})	.885
Indirect effect via number of seeds per pod ($r_{XY} P_{YW}$)	-.041
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	.044
Total (r_{XW})	.888
Effect of number of seeds per pod (Y)	
Direct effect (P_{YW})	.188
Indirect effect via number of pods per plant ($r_{XY} P_{XW}$)	-.193
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	-.093
Total (r_{YW})	-.098
Effect of seed weight (Z)	
Direct effect (P_{ZW})	.427
Indirect effect via number of seeds per pod ($r_{YZ} P_{YW}$)	-.041
Indirect effect via number of pods per plant ($r_{XZ} P_{XW}$)	.090
Total (r_{ZW})	.476

Table 15. Path coefficient analysis of the influence of X, Y
and Z upon yield (W), in families selected for Y at
all levels, A, M, and B, at Palmira, Medellin and
East Lansing in the first cycle of selection.

Type of effect	Coefficient

Effect of number of pods per plant (X)

Direct effect (P_{XW})	.868
Indirect effect via number of seeds per pod ($r_{XY} P_{YW}$)	-.143
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	.127
Total (r_{XW})	.852

Effect of number of seeds per pod (Y)

Direct effect (P_{YW})	.851
Indirect effect via number of pods per plant ($r_{XY} P_{XW}$)	-.146
Indirect effect via seed weight ($r_{YZ} P_{ZW}$)	-.209
Total (r_{YW})	.496

Effect of seed weight (Z)

Direct effect (P_{ZW})	.457
Indirect effect via number of seeds per pod ($r_{YZ} P_{YW}$)	-.388
Indirect effect via number of pods per plant ($r_{XZ} P_{XW}$)	.240
Total (r_{ZW})	.309

Table 16. Path coefficient analysis of the influence of X,
Y and Z upon yield (W) in families selected for
Z at all levels, A, M, and B, at Palmira, Medellin
and East Lansing in the first cycle of selection.

Type of effect	Coefficient
Effect of number of pods per plant (X)	
Direct effect (P_{XW})	1.300
Indirect effect via number of seeds per pod ($r_{XY} P_{YW}$)	-.364
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	-.143
Total (r_{XW})	.793
Effect of number of seeds per pod (Y)	
Direct effect (P_{YW})	1.224
Indirect effect via number of pods per plant ($r_{XY} P_{XW}$)	-.388
Indirect effect via seed weight ($r_{YZ} P_{ZW}$)	-.447
Total (r_{YW})	.389
Effect of seed weight (Z)	
Direct effect (P_{ZW})	1.065
Indirect effect via number of seeds per pod ($r_{YZ} P_{YW}$)	-.514
Indirect effect via number of pods per plant ($r_{XZ} P_{XW}$)	-.174
Total (r_{ZW})	.377

Table 17. Path coefficient analysis of the influence of X, Y, and Z upon yield (W) in families selected for X at all levels, A, M, and B, at Palmira, Medellin and East Lansing in the second cycle of selection.

Type of effect	Coefficient
Effect of number of pods per plant (X)	
Direct effect (P_{XW})	1.269
Indirect effect via number of seeds per pod ($r_{XY}\ P_{YW}$)	-.256
Indirect effect via seed weight ($r_{XZ}\ P_{ZW}$)	-.088
Total (r_{XW})	.925
Effect of number of seeds per pod (Y)	
Direct effect (P_{YW})	.971
Indirect effect via number of pods per plant ($r_{XY}\ P_{XW}$)	-.334
Indirect effect via seed weight ($r_{YZ}\ P_{ZW}$)	-.236
Total (r_{YW})	.401
Effect of seed weight (Z)	
Direct effect (P_{ZW})	.621
Indirect effect via number of seeds per pod ($r_{YZ}\ P_{YW}$)	-.368
Indirect effect via number of pods per plant ($r_{XZ}\ P_{XW}$)	-.178
Total (r_{ZW})	.075

Table 18. Path coefficient analysis of the influence of X, Y and
Z upon yield (W) in the families selected for Y at all
levels, A, M, and B, at Palmira, Medellin and East
Lansing in the second cycle of selection.

Type of effect	Coefficient
Effect of number of pods per plant (X)	
Direct effect (P_{XW})	1.568
Indirect effect via number of seeds per pod ($r_{XY} P_{YW}$)	-.455
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	-.214
Total (r_{XW})	.899
Effect of number of seeds per pod (Y)	
Direct effect (P_{YW})	1.414
Indirect effect via number of pods per plant ($r_{XY} P_{XW}$)	-.505
Indirect effect via seed weight ($r_{YX} P_{ZW}$)	-.447
Total (r_{YW})	.462
Effect of seed weight (Z)	
Direct effect (P_{ZW})	1.085
Indirect effect via number of seeds per pod ($r_{YZ} P_{YW}$)	-.584
Indirect effect via number of pods per plant ($r_{XZ} P_{XW}$)	-.308
Total (r_{ZW})	.193

Table 19. Path coefficient analysis of the influence of X, Y and Z upon yield (W) in families selected for Z at all levels, A, M, and B, at Palmira, Medellin and East Lansing in the second cycle of selection.

Type of effect	Coefficient
Effect of number of pods per plant (X)	
Direct effect (P_{XW})	1.203
Indirect effect via number of seeds per pod ($r_{XY}\ P_{YW}$)	-.166
Indirect effect via seed weight ($r_{XZ}\ P_{ZW}$)	-.174
Total (r_{XW})	.863
Effect of number of seeds per pod (Y)	
Direct effect (P_{YW})	.936
Indirect effect via number of pods per plant ($r_{XY}\ P_{XW}$)	-.213
Indirect effect via seed weight ($r_{YZ}\ P_{ZW}$)	-.365
Total (r_{YW})	.358
Effect of seed weight (Z)	
Direct effect (P_{ZW})	.941
Indirect effect via number of seeds per pod ($r_{YZ}\ P_{YW}$)	-.363
Indirect effect via number of pods per plant ($r_{XZ}\ P_{XW}$)	-.223
Total (r_{ZW})	.355

Tables 14, 15 and 16 show the direct and indirect effects of components upon yield, in families selected for number of pods per plant, number of seeds per pod and seed weight respectively at the three locations under study, during the first cycle of selection. Results for the second cycle of selection are presented in Tables 17, 18 and 19.

A general pattern of effects is detected during the two cycles of selection. The influence of number of pods upon yield is the most important among the yield components, followed by number of seeds per pod and seed weight.

To illustrate this situation, let us take the case of families selected for number of seeds per pod (Y) during the first cycle of selection presented in Table 15. The correlation between number of pods and yield is made up mostly of direct effects indicating, therefore, the importance of this character in determining seed yield; the first effect of number of seeds per pod upon yield is also of great magnitude, although some negative influence was registered indirectly especially via seed weight. An examination of the correlation of seed weight with yield reveals that its direct effect has importance in influencing seed yield, although it is of smaller magnitude than the effect of X or Y upon W. As was expected, a negative indirect effect through number of seeds per pod is observed.

It may be seen in Table 18, with respect to families selected for number of seeds per pod in the second cycle, that in general a pattern similar to that in the first cycle is observed, as far as the order of importance of direct influences upon yield is concerned. The magnitude of the direct effect of number of seeds per pod upon yield increased a great deal as compared with the first cycle, indicating the influence of selection in raising the magnitude of direct effects of selected components upon yield.

Negative indirect effects were also greater as might have been expected; the negative influence via number of pods per plant was larger than the one via seed weight due to the negative association between XY and the great magnitude of the direct effect of number of pods upon yield.

Although the correlation coefficient between number of pods per plant and seed yield is more or less the same as in the first cycle in families selected for Y, its direct effect upon yield is of higher magnitude; however, an indirect negative influence upon yield is detected through number of seeds per pod, because of the negative correlation between X and Y and the importance in magnitude of the path coefficient between Y and W.

The low value of the correlation coefficient between Z and W is made up mostly of negative indirect effects, especially via seeds per pod although the effect via number of pods also has

appreciable value. The direct effect of seed weight upon yield
is nevertheless of great importance in determining yield.

As a general pattern it could be said that the direct effect
of a component upon yield increased in magnitude when selection
pressure was applied for that component.

Table 20 shows a path coefficient analysis of the influence
of components of yield upon yield and the influence of number
of leaflets and size of the leaflets upon yield components at
Palmira and Medellin in the first cycle of selection in families
selected for number of leaflets per plant (N). Similar sets of
path coefficients and indirect effects are presented in Table
21 for families selected for leaflet size (S).

Table 20. Path coefficient analysis of the influence of X, Y, and Z upon yield (W) and the influence of N and S upon yield components, in families selected for N at all levels, A, M, and B at Palmira and Medellin in the first cycle of selection.

Type of effect	Coefficient
Effect of number of leaflets (N) upon X	
Direct effect (P_{NX})	.584
Indirect effect via leaflet size (r_{NS} P_{SX})	.022
Total (r_{NX})	.606
Effect of leaflet size (S) upon X	
Direct effect (P_{XS})	-.147
Indirect effect via number of leaflets (r_{NS} P_{NX})	-.087
Total (r_{SX})	-.234
Effect of number of leaflets (N) upon Y	
Direct effect (P_{NY})	.148
Indirect effect via leaflet size (r_{NS} P_{SY})	-.025
Total (r_{NY})	.123
Effect of leaflet size (S) upon Y	
Direct effect (P_{SY})	.166
Indirect effect via number of leaflets (r_{NS} P_{NY})	-.022
Total (r_{SY})	.144
Effect of number of leaflets (N) upon Z	
Direct effect (P_{NZ})	-.116
Indirect effect via leaflet size (r_{NS} P_{SZ})	-.074
Total (r_{NZ})	-.190
Effect of leaflet size (S) upon Z	
Direct effect (P_{SZ})	.502
Indirect effect via leaflet size (r_{NS} P_{NZ})	.017
Total (r_{SZ})	.519

Table 20 (Continued)

Type of effect	Coefficient
Effect of number of pods (X) upon W	
Direct effect (P_{XW})	.982
Indirect effect via number of seeds ($r_{XY} P_{YW}$)	.125
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	-.194
Total (r_{XW})	.913
Effect of number of seeds (Y) upon W	
Direct effect (P_{YW})	.341
Indirect effect via number of pods ($r_{XY} P_{XW}$)	.359
Indirect effect via seed weight ($r_{YZ} P_{ZW}$)	-.166
Total (r_{YW})	.534
Effect of seed weight (Z) upon W	
Direct effect (P_{ZW})	.376
Indirect effect via number of pods ($r_{XZ} P_{XW}$)	-.508
Indirect effect via number of seeds ($r_{YZ} P_{YW}$)	-.151
Total (r_{ZW})	-.283

Table 21. Path coefficient analysis of the influence of X, Y, and Z upon yield (W), and the influence of N and S upon yield components, in families selected for S at all levels, A, M, and B at Palmira and Medellin in the first cycle of selection.

Type of effect	Coefficient
Effect of number of leaflets (N) upon X	
Direct effect (P_{NX})	.757
Indirect effect via leaflet size ($r_{NS} \, P_{SX}$)	-.014
Total (r_{NX})	.743
Effect of leaflet size (S) upon X	
Direct effect (P_{XS})	.070
Indirect effect via number of leaflets ($r_{NS} \, P_{NX}$)	-.147
Total (r_{SX})	-.077
Effect of number of leaflets (N) upon Y	
Direct effect (P_{NY})	.119
Indirect effect via leaflet size ($r_{NS} \, P_{SY}$)	-.019
Total (r_{NY})	.100
Effect of leaflet size (S) upon Y	
Direct effect (P_{SY})	.095
Indirect effect via number of leaflets ($r_{NS} \, P_{NY}$)	-.023
Total (r_{SY})	.072
Effect of number of leaflets(N) upon Z	
Direct effect (P_{NZ})	-.186
Indirect effect via leaflet size ($r_{NS} \, P_{SZ}$)	-.094
Total (r_{NZ})	-.280
Effect of leaflet size (S) upon Z	
Direct effect (P_{SZ})	.485
Indirect effect via leaflet size ($r_{NS} \, P_{NZ}$)	.036
Total (r_{SZ})	.521

Table 21 (Continued)

Type of effect	Coefficient
Effect of number of pods (X) upon W	
Direct effect (P_{XW})	1.047
Indirect effect via number of seeds ($r_{XY} P_{YW}$)	-.002
Indirect effect via seed weight ($r_{XZ} P_{ZW}$)	-.113
Total (r_{XW})	.931
Effect of number of seeds (Y) upon W	
Direct effect (P_{YW})	.244
Indirect effect via number of pods ($r_{XY} P_{XW}$)	-.011
Indirect effect via seed weight ($r_{YZ} P_{ZW}$)	-.098
Total (r_{YW})	.135
Effect of seed weight(Z) upon W	
Direct effect (P_{ZW})	.331
Indirect effect via number of pods ($r_{XZ} P_{XW}$)	-.358
Indirect effect via number of seeds ($r_{YZ} P_{YW}$)	-.072
Total (r_{ZW})	-.099

It is interesting to notice the very strong association between characters specified by numbers, as number of leaflets and number of pods per plant, and also between characters whose measure is size, size of the leaflets and seed size.

The high correlation between number of leaflets and number of pods is made up mostly of direct effects, indicating the importance of N in determining number of pods, with the latter exerting a strong direct influence upon number of pods in families selected for N and positive in families selected for S. However, in both cases these effects are of small magnitude and may be regarded as unimportant.

The direct and indirect effects of number of leaflets per plant and size of the leaflets upon number of seeds are quite low.

The low and negative correlation between number of leaflets and seed weight is made up of small direct and negative effects that may be considered negligible. On the contrary, the high correlation between leaflet size and seed size acts almost completely through direct effects of the former upon the latter. Even though seed size shows a small negative correlation with yield, its direct influence upon yield is positive, as it should be. However, the negative correlation is composed mainly of negative indirect effects through number of pods, due to the fact that seed size was negatively correlated with number of pods which in turn has a strong direct effect upon seed yield.

It is necessary to point out that the negative correlations between number of pods and seed size were of higher magnitude than the correlations between number of seeds per pod and seed size when selection pressure was applied to number of leaflets and size of leaflets. This situation could result from the strong positive associations between N and X and S and Z. In turn, N and S exhibit negative relationships, the same being true as far as the associations between N and Z and S and X are concerned.

DISCUSSION

A path coefficient is a standarized partial regression coefficient,
and in that way measures the direct effect of one variable upon
another and permits the separation of the correlation into direct
and indirect effects. To apply this method the cause and effect
relationship must be known. Yield of beans is a product of its
components, therefore, the requirement of cause and effect is ful-
filled.

The results of the path analysis for yield and its components
indicate that number of pods per plant exerts the greatest influ-
ence in determining seed yield. This signifies that selecting for
a higher number of pods should increase yield. However, some
negative influence upon yield is registered via number of seeds
per pod which deserves some attention when selection pressure
is exerted upon number of pods.

The direct effect of number of seeds per pod is of appreciable
magnitude especially in families selected for this character,
indicating its strong influence upon yield, when the other two
components are held constant. However, some negative indirect
effects mask the direct effect of seeds per pod upon yield, the
chief ones of which function through seed weight, as was expected.

The correlation coefficient between seed weight and yield is in
general of low magnitude except when selection was applied to seed
weight, the degree of association being then of much greater
magnitude. However, the path analysis reveals that the direct

effect of seed weight is of considerable importance in deter-
mining yield. The low value of the correlation is made up
mainly of indirect effects especially through number of seeds,
although in cases in which selection was made for numbers of
pods the negative influence of the latter is mostly of negligible
magnitude. This means that selection for seed size alone does
not have a very strong influence upon yield; selection should be
conducted either for seed weight and number of pods or seed
weight and number of seeds per pod depending on the environment
in which the selections are going to be made.

The correlation between number of leaflets and number of
pods shows that it is made up mainly of direct effects, indi-
cating that the number of leaflets has great importance in deter-
mining number of pods which in turn has primary importance in
determining seed yield.

Leaflet size has strong influence in determining seed size as
shown by a path coefficient of high magnitude. The indirect
effect are small and non-important.

The influence of number of leaflets and leaflet size in
determining number of seeds per pod is of low magnitude at least
in the present study. This may be due to the fact that the path
analyses were made with data coming from families selected for
number and size of leaflets; these two characters influence, as
was said before, number of pods and seed size respectively, the

seed number thus being dependent on the magnitude of the other two yield components.

The findings of the direct and indirect effects of the yield components upon yield and in turn the effect of number of leaflets and size of leaflets upon yield components agreed with those discussed in the second part of this thesis about compensation among yield components. It was said that the magnitude of each component depends on the total amount of resources available in a common pool and its distribution among the components, this distribution depending on the genetic make-up of each one of the components and on their developmental sequence. It was also proposed that the distribution of resources could be determined even before the floral stage of development starts, the greater share being appropriated by the component with more genes for high expression, the remaining resources being distributed between the other two components according to their genetic constitution.

The fact that number of leaflets determines to a large extent the number of pods suggests that the share in the distribution among yield components was already fixed at the late vegetative stage prior to floral initiation. The same pattern is apparent in the case of seed size; size of the leaflets has a strong direct influence upon seed size suggesting that according to the genetic make up of Z, the genes that condition the expression of this character are "turned on" at an earlier stage of growth of the plant.

Number of seeds per pod may be influenced through the relaion-
ship between number of leaflets and size of the leaflets, which
in turn is reflected in number of pods and size of the seed.

SUMMARY AND CONCLUSIONS

The results of two cycles of recurrent selection in a bean hybrid population are described. This population originated from intra-specific crosses of _Phaseolus vulgaris_ variety Algarrobo by variety Michelite; Algarrobo is from Colombia, South America, and Michelite from Michigan, U.S.A. These two varieties are contrasting in several vegetative and reproductive characteristics.

The aim of this investigation was to obtain fuller knowledge of the response to selection components of complex traits, and also to evaluate the relationships among selected and non-selected components, these relationships being of definite importance in the phenotypic expression of the complex trait.

This study was carried out at three different locations; two of them in Colombia, S.A. and the third in East Lansing, Michigan. These locations differ in climatic conditions, such as temperature, rainfall, day-length, and length of growing season.

Selection in Colombia was practiced independently for leaf area components, namely number of leaflets per plant (N), and leaflet size (S), and for yield (W) components namely number of pods per plant (X), number of seeds per pod (Y), and seed weight (Z). In East Lansing selections were made for yield components and also for yield itself. Selections were made at three levels

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of expression for all locations, high (A), intermediate (N),
and low (B).

The results obtained in this study can be summarized as
follows:

1. Progress was made from one cycle to another for each one
   of the components of the complex traits, both toward high
   and low levels of expression.

2. The rate of progress for each particular component at
   each level of expression was not the same at all locations.
   The involvement of genes that are expressed differently at
   different locations is inferred; also the better adaptedness
   of the parental types at certain locations seems to have
   played a role in character-location association.

3. Progress for yield itself was not really made. Progress
   in the values of individual components was obtained,
   but the gain in one component was at the expense of another
   or other components, giving through their multiplicative
   interaction quite similar results in seed yield.

4. The unselected components showed negative relationships with
   the selected ones, the magnitude of the association depending
   upon the response to selection; however, if one of the un-
   selected components responded too far in the direction
   opposite to the selected one, the third component reverted
   and varied in the same direction as the selected one, con-
   ferring in this way a moderate level of buffering upon yield
   itself.

5. The correlation coefficients obtained supported the findings just described. Assuming that the correlations were genetic they could be originated by several factors such as, linkage, or pleiotropic effects; but negative correlations can also result when characteristics share a common pool of metabolic resources for their development, generated by a given set of genes.

6. The results showed that correlation coefficients among the yield components changed in sign from one cycle to another in several instances. Also the correlations in the total number of families present differences in sign as compared with the selected ones. These findings are in good agreement with results obtained by other authors, and strongly suggest that the correlations among yield components are not truly genetic in the sense of linkage or pleiotropism inasmuch as they could be changed by selection pressure and/or environmental conditions. The data also furnish evidence indicating that mainly independent genetic systems are controlling each one of the yield components in beans.

7. Two hypothesis are presented to account for the negative correlations. The first one states that the different genetic systems of X, Y and Z share a common pool of metabolic resources, the amount of these resources being controlled by genes, and their distribution depending on the interaction

between the genotype of each component and the genes that control
the resources. This interaction, which takes the form of a "turning
on" process, occurs prior to floral development and the share that
each component receives is fixed at that time. The second
hypothesis would also postulate a common pool of developmental
resources to be shared by X, Y and Z. The relationships among
yield components depend on the views that (1) components follow
a sequential pattern of development, (2) each one has its own
genetic system and (3) they are sufficiently flexible in develop-
ment to be responsive to the amounts of resources available for
their growth. If a proportionately greater share of the resources
were used in producing high X, a proportionately lesser amount
would be available for producing high Y values, or possibly Z
values. In selecting for a component such as Z, its high ex-
pression would depend on plentiful resources, which in turn implies
genotypes of low level of expression for Y and X.

8. Neither one of the hypotheses presented precludes the possibility
that by artificial means the pool of resources can be increased
and that by selecting for genes that give high level of expression
to each one of the components when resources are unlimited, the
possibility of maximizing yield could be realized.

9. Direct and indirect effects of the components upon the complex
traits were analyzed by means of path coefficients. The results
show that N has a direct positive effect upon X, and the main
effect of S is upon Z. In turn, X exerts the greatest influence
upon seed yield, followed by Y, then by Z. Indirect negative

effects were detected and discussed.

10. Selection for two components at the same time are suggested for

each location.

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